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CHIMÆROID FISHES AND THEIR DEVELOPMENT

BY

BASHFORD DEAN
PROFESSOR OF VERTEBRATE ZOOLOGY, COLUMBIA UNIVERSITY

WASHINGTON, D. C.
PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
1906

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BY

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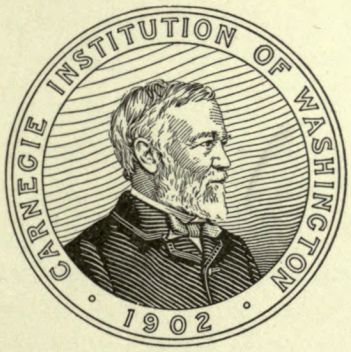

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ERRATA.

Page 11, for Regnè read Règne.
Page 30, second column, after Rhinochimæra pacifica, for 3 read 33.
Page 36, fig. 20, for Rhinochimæra read Harriotta (?).

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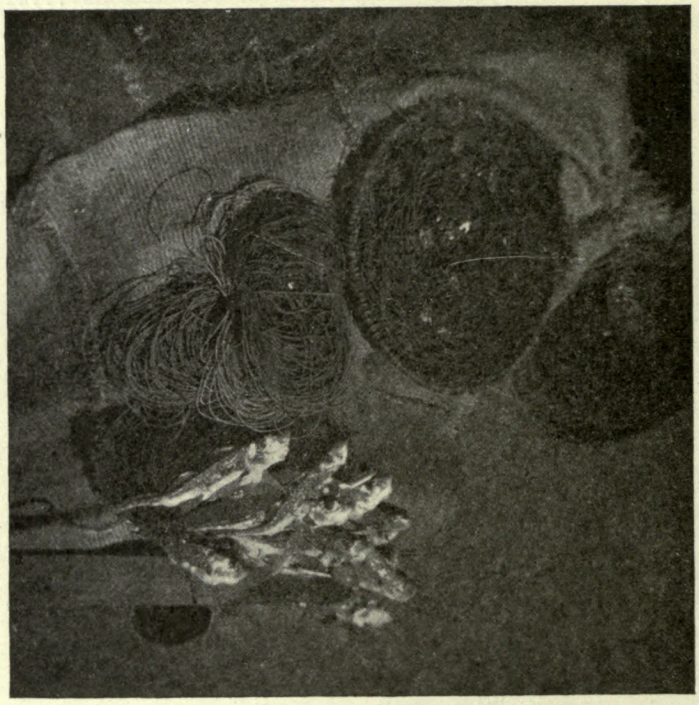


A day's catch of Rat-fish, Chimæra colliei, on the beach at Pacific Grove (near Monterey), California. Beside the fish are the float-lines and baskets with trawl.

CHIMÆROID FISHES AND THEIR DEVELOPMENT.

BY BASHFORD DEAN,

Professor of Vertebrate Zoology, Columbia University.

CHIMÆROID FISHES AND THEIR DEVELOPMENT.

UNIV. OF CALIFORNIA

INTRODUCTION.

Chimæroid fishes, a group representing some of the oldest and simplest of backboned animals, are considered in the present memoir with especial regard to their relationship and descent. To this end, attention has now been paid to the plan of their embryonic development, and upon this side evidence has been obtained which, whether of major or minor importance in the study of descent, has at least the interest of newness. For to the embryologist Chimæroids have until recently remained practically unknown, and they are thus the only vertebrate group of their anatomical importance—if ranked as a subclass—to have escaped investigation.

On the other hand, from the standpoints of comparative anatomy and paleontology these shark-like fishes have received considerable notice, and they have figured in publications of the past half-century as the "most primitive vertebrates," or, more precisely, as the least modified descendants of the ancestral cranium- and jaw-bearing vertebrate. And in such a rôle (which I now believe is only partially deserved) they have been given especial importance in problems of descent.

The evidence which has been brought forward to demonstrate the primitive nature of Chimæroids is based in part upon the findings of paleontology ; it is, moreover, as one frankly admits, supported by anatomical facts which are broad in range and which have in many instances been provided by masters in morphology. The substance of this evidence is that Chimæroids, although shark-like, are nevertheless widely distinct from the shark, and that they represent a lower plane in piscine evolution. As an aid to subsequent reference, the grounds for this conclusion may now be summarized.

PALEONTOLOGICAL.

Chimæroids are believed by some to be older than sharks. Their fossils, as Walcott maintains, occur among fragments of "fish" plates in the Ordovician (Lower Silurian) sandstones. Sharks, on the other hand, do not occur—that is, unquestionably—before the Upper Silurian. Probable it is that Chimæroids lived during the Lower Devonian and, judging from their dental plates, these forms, if Chimæroid, were highly differentiated, even at this early period. Moreover, according to the studies of Jaekel, paleozoic Chimæroids provide the evolutional stages from certain archaic armored "fishes" to the shagreened sharks.

RECENT.

Many characteristic structures of living Chimæroids have been referred to as indicating the primitive nature of the group. The following may be cited:

Dentition and dermal defenses, by Jaekel (1901), who maintains that the dental plates are primitive or "statodont," *i. e.*, the ancestral condition of the "lyodont," or successional teeth of the later sharks. They have thus, if I understand Jaekel's view correctly, become greatly subdivided, so as to produce the cuspid teeth of sharks. So, too, the larger integumental plates of ancient Chimæroids are believed to have given rise to cuspid scales, and a somewhat similar view was expressed by Pollard (1891). According to Schauinsland (1902), the scales of Callorhynchus are of so primitive a nature as to be directly compared to those of the earliest Silurian "sharks." Finally, Reis (1895) suggests that the curious unpaired tooth of mesozoic Chimæroids finds its homologue only in the ancient Acanthodia.

Vertebral column, with delicate ring "vertebræ," characteristic of Chimæroids, is, according to Schultze (1817), but the next stage above the notochordal condition of the lamprey; to Hasse (1879) it represents a polyspondylous condition ancestral to the diplospondyly of the simplest living sharks; to Gegenbaur (1901) "less differentiated"; to Howes (1902) a purely "chordal type"; to Meyer (1886) "possibly primitive"; to Rabl (1901) a column which has "not developed centra."

Cranium and arches.—According to Cope (1870), the autostylism of Chimæroids is in itself primitive, in spite of the evidence of its secondary character, which has been assumed on comparative anatomical grounds from the time of Johannes Müller (1838). So, too, Kitchen Parker (1883) inclines, though doubtfully, to its primitive autostyly; and Gadow (1886) appears to have a similar view in stating that dipnoans were descended from a "simple autostylic form." The curious labial cartilages are regarded by Howes (1891) and others as homologous with those of hag-fishes. And connected with these the *levator anguli oris*, according to Reis (1896), suggests closely the condition in Acanthodian sharks. Allis (1898) also suggests that the jaw muscle (adductor) is of a primitive type (*i. e.*, interbranchial), and in this he follows distinctly the more general conclusions of Vetter (1878), which are, indeed, in the latest time confirmed by K. Fürbringer. The second branchial arch, it may here be mentioned, has been referred to several times (*v. infra*) as retaining archaic features. The labial cartilages, furthermore, are said to be primitive, inasmuch as they represent the most perfect condition of preoral gill-arches known among recent gnathostomes (K. Fürbringer, 1903, and Schauinsland, 1903); and a presymphyseal cartilaginous element is regarded as a primitive copula between the mandibular and a premandibular arch. In fact, the entire series of copulæ is archaic (Gegenbaur, 1901).

Ribs are absent, a primitive character, according to Goeppert (1895).

Fin structures are of peculiar interest. According to Jeffrey Parker (1886), the Chimæroid is the only vertebrate to retain rudiments of a third pair of limbs. Its paired limbs furnish, according to Gegenbaur, M. Fürbringer, and Braus, evidence of the origin of the paired limbs from gill-arches. In this connection Howes (1886)

maintains that the paired fins of Chimæra are ancestral to those of sharks and dipnoans. Rabl (1901) also refers, but in a different aspect, to the primitive nature of the fins of Chimæra. By several writers the unpaired fins are regarded as primitive. The fin spine, as Reis (1896) maintains, shows the granular calcification of the mesozoic Ischyodus. The mixipterygia are "of less compound construction" (Jungersen, 1898) than those of sharks.

Brain, nerves, and sense organs have received considerable attention. Valentin (1842) states that in its brain Chimæra is intermediate between cyclostomes and plagiostomes, and his view is shared, more or less distinctly, by Johannes Müller, Miklouchо-Macleay, Gegenbaur, Wilder, and M. Fürbringer. To Burckhardt (1893) the Chimæroid brain suggests characters allied on the one hand to the primitive sharks, on the other to the lower ganoids, and according to Studnička (1895) the forebrain is nearer the primitive form of the selachian brain than even that of Notidanid. Jaekel (1902) holds also that in Chimæra, alone among fishes, there appears an epiphyseal opening in the cranial roof. In the matter of cranial nerves Cole (1896) states that "Chimæra is unrivalled among vertebrates, first, for the ease with which its nerves may be dissected and, second, for the almost ideal results that may be attained," as well as for the peculiarity of independent nerve roots, "archaic and perhaps primitive in type." Similarly, Fürbringer (1897) comments upon the peculiar conditions of the nerves of the occiput. Collinge (1896) notes also the simplicity of the mucous-canal system, which, he believes, separates widely Chimæroids and sharks. From the standpoint of the auditory organ Retzius (1884) places Chimæroids in the ancestral line of the modern elasmobranchs. Gegenbaur (1901), finally, notes that the flattened cord is primitive, like that of cyclostomes.

Visceral peculiarities have also been given considerable notice. Thus Huxley (1872) refers to the "almost undeveloped gastric division of the alimentary canal, [and] the relatively small and simple heart." Gegenbaur (1901) is inclined to regard the few turns of the spiral intestinal valve as the ancestral condition of the gut of Lepidosteus and Ceratodus. Leydig (1851), followed by Mazza and Perugia (1894), suggests that the many small brown glands of the rectum represent the ancestral condition of the digitiform appendix of sharks. Redeke (1899) maintains that in the structure of the kidney Chimæroids are primitive, since, among other features, they retain a remarkable metamerism and have not the modified Geschlechtsniere of sharks.

The foregoing are the principal lines of argument in favor of the primitive position of Chimæroids. Whether they can be maintained in the light of additional evidence, notably on the side of embryology, is a question which will be discussed in the present memoir.

To summarize the problem: Are the Chimæroid fishes the least modified descendants of the primitive gnathostome? Or are they, on the contrary, degenerate, specialized, or widely modified? Are they, in other words, close to ancestral forms which gave rise to sharks, with which they are obviously associated—or are they but modifications of the shark-like form? In spite of the formidable list

of citations as to their phyletic position, every investigator will admit that Chimæroids have been but little studied—surprisingly little studied, if we consider the morphological problems which they have trenched upon And in this regard we may safely conclude that the obstacle in the way of the investigator has often been a simple one—lack of material for research. For, until recently, good material of Chimæra was relatively rare. As a deep-water form, it was taken only by special fishermen in special localities, and even then, since it was not a food-fish, it found its way rarely to a market and still more rarely to a laboratory. This, then, has been an obvious reason why embryological material was not early described. It may finally be mentioned that fossil Chimæroids, so important to the general discussion, are rare, and, with very few exceptions, fragmentary.

Recent Chimæroids are included in 4 genera and about 25 species. An idea of their distribution and size may be had by reference to the following table:

TABLE A.— *Kinds, Localities, and Approximate Sizes of Recent Chimæroids.*

Genus and species.	Reference.	Locality.	Size (±).
			Meters.
Callorhynchus callorhynchus.....	Gronovius, 1754, Mus. Ichthyol., I, p. 59, plate IV, figs. 1 and 2. Linn., as species, Syst. Nat., Zoophylae, 10 ed., p. 236. (Followed by Swainson, Guichenot, and others.)	Australia.....	0 .85
(?=antarcticus).....	Lacépède, 1799, Hist. Poiss., I, p. 400, plate XII. (Followed by Swainson, Guichenot, and others.)	Australia, S. America.....	
(?=australis).....	Hobson (1840), Tasmanian Jour. Science, vol. 1.	Australia.....	.....
	Shaw, Gen. Zool., V, Pt. II, 368, pls. CLVII and CLVIII. ? Immature specimen.	.....	.75
(?=peronii).....	Duméril, 1865, Hist. Nat. Poiss. I. Elasmobranchs, 694–695. Immature specimens.	Patagonia	.....
(=elephantinus).....	Gronow. Syst., ed. Gray, 1854, p. 15....	.....	.....
capensis	Duméril, op. cit., 695–696	S. Africa.....	.85
tasmanius.....	Richardson, 1841, Proc. Zool. Soc. and Trans. Zool. Soc., III, 174.	Tasmania.....	.95
(?=C. milii)... ...	Bory St. Vincent, Dict. Class. Hist. Nat., vol. III, p. 62, plate v.	Australia.....	.....
smythi	Bennett, Fishes of Capt. Beechey's Voyage, p. 75, plate XXII, fig. 3.	Concepcion.....	.....
dasycaudatus.....	Colenso, 1878, Trans. N. Z. Inst., vol. XI., pp. 299–300, plate XVII.	New Zealand....	1.10
argenteus.....	Philippi, 1892, An. Mus. Nac. Chile, Zool., p. 11, tab. v, fig. 1. Immature specimen (39 cm.).	Chile.....	.....
Harriotta*.....	Goode & Bean (1894), Proc. U. S. Nat. Mus., vol. XVII, pp. 471–472.	.....	. .....
raleighana	Ibid., pp. 472–473, plate XIX.....	N. Atlantic.....	.70
Rhinochimæra.....	Garman (1901), P. N. Eng. Zool. Club, vol. I, II, pp. 75–77.	.....	.....
pacifica.....	Mitsukuri (1895), Zool. Mag. Tokyo, vol. VII, p. 2.	Japan...	1.30
indica	Garman S. (1899) (=Callorhynchus indicus), Mem. M. C. Z., vol. XXIV, pp. 20–21. Named from egg-case only.	Indian Ocean.....	.....

*By any remote possibility could this have been *Callorhynchus centrina*, which Gronow described from a specimen which he saw "in museo cl. Gaubii, Lugd. Batav."? (Syst., ed. Gray, 1854, pp. 15–16.) His description suggests Harriotta rather than Rhinochimæra, since "habitat in Oceano Americano." It is hardly conceivable, however, that Gronow should have happened across this rare form, and from the general vagueness of the description and in view of the absence of the type specimen the name *Callorhynchus centrina* should be cast out of the systematic list.

TABLE A.—*Kinds, Localities, and Approximate Sizes of Recent Chimæroids*—Continued.

Genus and species.	Reference.	Locality.	Size (±).
			Meters.
Chimæra	Linnæus, Mus. Regis Adolph. Frid., vol. I, p. 53. Syst. Nat., ed. x, 1758, vol. I, p. 236.	.....	.....
affinis	Capello (1868), Jour. Math. Phys. e Nat. Lisb., vol. LV, p. 314, plate III.	Coast of Portugal	(0.70)
(?=abbreviata)	Gill (1884), Proc. U. S. Nat. Mus., vol. VI, p. 254.	Middle Atlantic	.....
colliei	Bennett (1839), Fishes, in Zoology of Capt. Beechey's Voyage, p. 71, plate XXIII.	Pacific Coast of U. S.	.70
(=Hydrolagus colliei)	Gill (1862), Proc. Acad. Nat. Sci. Phila., p. 331; cf. Dean, J. Sci. Coll. Tokyo (1904), vol. XIX, art. 3, p. 8.	.....	.....
(=neglecta)	Waite (1898), Ref. in "Thetis," N. S. Wales Fisheries, p. 56.	.....	.....
mitsukurii	Dean (1904), Jour. of Sci. College, Tokyo, Japan, vol. XIX, art. 3, pp. 6–9.	Japan	.60
monstrosa	Gunner (1763), Det. Trondhiemske Selskabs Skrifter, vol. II, p. 270, plates V, VI.	North Atlantic and Mediterranean. (?Cape of Good Hope.)	.80
(=argentea)	Ascan., Icones rerum natur., plate XV.	North Atlantic	.....
(=Cal. atlanticus)	Gronow 1854, Syst., ed. Gray, pp. 16–17.	Atlantic	.....
(=borealis)	Shaw, Gen. Zool., vol. V, pt. 2, p. 365, plate 157.	North Atlantic	.....
(=cristata)	Faber, Naturgesch. Fische Islands, p. 45. Based on abnormal specimens.	North Atlantic	.....
mediterranea	Risso, 1826. No. 151. Nat. Eur. Merid., t. III, p. 168.	Mediterranean	.....
(?C. Bathyalopex) mirabilis.	Collett, 1904. Chr. Videnkabs-Selskabs Forh., No. 9, pp. 5–6. Based on young specimens.	Faröe	.....
ogilbyi	Waite (1899), Austr. Museum Mem., IV, p. 48, plate VI.	Australia	.85
phantasma	Jordan & Fowler, 1903, Proc. U. S. Nat. Mus., vol. XXVI, p. 669 (nec Jordan & Snyder, 1900, Proc. U. S. Nat. Mus., vol. XXIII, p. 338 (1901)).	Japan	1.00
plumbea	Gill (1878), Bull. Phil. Soc. Washington, vol. II, p. 182.	North Atlantic	1.00
purpurascens	Gilbert, MS.	Hawaii and Japan	1.75
vaillanti	Dean, MS. (type in Jardin des Plantes, No. 2557.)	Cape of Good Hope	.75

(Since the above was in type the writer has seen in Japan two new species of Chimæra. These will shortly be described by Mr. Tanaka in the Jour. Sci. Coll.)

DATA REGARDING COLLECTING.

It has long been known that Chimæroids deposit large eggs, and that these are inclosed in dart-shaped capsules, brown, heavy, somewhat after the fashion of sharks, and resembling outwardly a frond of a giant Fucus. But further than this nothing appears to have been ascertained as to their habits in breeding. At the most, it was understood, from the complicated character of the capsule, that the eggs were carried in the oviducts for a considerable time.

This inference is clearly important to one who seeks to collect embryonic stages. For, given unlimited time and a locality yielding numerous specimens of Chimæra, one could evidently secure gravid females, and from these the requisite number of mature egg-capsules. Thereafter one would have merely to incubate the eggs,

either in aquaria or in cases floating or sunken, and then, from time to time, select the developmental stages.* This mode of procedure, however, was not without practical difficulties, as the present writer found to his cost. In the first place, he was for several years unable to locate a region in which Chimæra could be taken constantly and plentifully. To this end several points along the European coast were considered in vain. In the bay of Naples Chimæra is uncommon, contrary to what one is led to infer from the notes given by Costa (1854); for it was found (1891) that but few specimens could there be obtained, even through the excellent collecting facilities offered by the Stazione. Messina is said to be a favorable locality, but upon inquiry it was ascertained through Cav. LoBianco that even there Chimæra was erratic in its appearance, and that months might elapse before many specimens could be collected. At Nice, also, inquiry showed that similar conditions prevailed. The coast of Portugal gave the best promise of abundant material, but the writer found, during a visit in 1891, that collecting facilities were unattainable. There were still to be considered the collecting possibilities of the coast of Norway, where, indeed, Collett (1875) had already obtained an egg of Chimæra, when it was learned that a species of Chimæra, *C. colliei*, was taken in considerable numbers on the Pacific coast of the United States. It was next ascertained from Dr. Tarleton H. Bean that this form could be taken in the waters of Puget Sound, and that it was especially abundant in the neighborhood of Port Townsend. Here, moreover, it occurred in relatively shallow water, and Dr. Bean had seen specimens of these "rat-fish," as they are locally known, swimming about near the wharves. Puget Sound was accordingly visited, Columbia University sending out a party† with a view to collect, among other desiderata, embryonic material of Chimæra; and during a summer (1896) efforts were made to secure both the eggs and the living fish. The latter were abundant. About a score of females were examined, but in no case were eggs obtained. From the condition of the ovaries it was inferred that the spawning season had passed.

Efforts were next made to secure eggs by dredging, but this means also proved in the end fruitless. It resulted, nevertheless, in collecting egg-capsules, and in several localities. At one point in Discovery Bay as many as sixty capsules were dredged (6 fathoms) during a single morning, but these, as in other instances, were found to be empty. The majority of the capsules were broken and frayed, and bore evidence of having been in the water many months. Every effort, however, failed to secure capsules containing eggs. Possibly they might have been secured if dredging in deeper water could have been carried on, for in no case was material obtained from deeper than 10 fathoms. But it was remarkable that so many empty cases should be taken close together, and in shallow water, if they had not

*Since these pages were written Prof. Schauinsland has published an extremely valuable memoir on the development of Callorhynchus, but he has given no notes regarding the manner in which eggs were secured at Chatham Island, or how these embryos were reared. They appear to have been collected separately, since he describes no stage earlier than gastrula.

†In this, as in similar cases, the University was indebted to the fund donated by Charles H. Senff, Esq.

been deposited in the neighborhood. It was still, of course, possible that they had been sifted into the present position, perhaps by currents, from a greater depth, or that the egg-bearing capsules were actually close to the empty ones and had not been dredged. The latter alternative would clearly be suggested if the eggs, like those of certain species of rays, were deposited in beds, thrust into sand or mud deeper than the reach of the dredge—a possibility which, *a priori*, seemed favored by the dart-like shape of the Chimæroid egg-case. But even this suggestion proved in the end valueless, for experiments showed that no eggs were to be taken by the use of a weighted dredge (one which cut deep into the muddy bottom), even when used in the especial spot which had yielded the greatest number of empty capsules.

The first eggs of Chimæra were obtained on the California coast during the latter part of the same summer (1896). The writer is greatly indebted to President Jordan for his invitation to visit the Hopkins Marine Laboratory at Monterey, and for his suggestion as to the value of the Chinese fisher-people as zoölogical collectors. Among the fishermen Ah Tack Lee was found to be of the utmost service, skilful, persevering, accurate in locating Chimæra grounds, and keen in observing. He had even noticed that Chimæra has the curious habit of carrying temporarily its pair of eggs hung freely in the water attached only by elastic threads, and that the terminal filament of the egg-case is provided with an end-bulb which secures its attachment.

A few words further regarding collecting. During the first summer, between July 22 and September 12, there were collected 300 males and 139 females. Of the latter 15 carried eggs. Each gravid female was found to contain two eggs in practically the same stage of development. The plan pursued was to take those eggs in which the capsule was sufficiently formed (18 out of 30 eggs) and place them in a case, which was then sunk, attached to a buoy, in water of about 30 feet. Of the number of eggs thus incubated, half were opened for the earlier stages; the rest, unfortunately, were lost, a storm having carried away buoy and hatching-case. It was none the less clear, however, that the method was successful, and it was evidently but a matter of time before a fairly complete series of embryos could be collected. A new and stronger buoy was therefore established off the Chinese village, and from that time to the present, allowing always for periods of laxity, the fisher-people, influenced by Ah Tack, have been collecting eggs. The only practical difficulty was found to be the suitable fastening of the hatching-cases, for at various times about 150 eggs have been lost.

The writer is particularly indebted to Dr. Ray L. Wilbur, of the department of physiology of Leland Stanford University, for his kind coöperation in the collecting work. Dr. Wilbur paid a number of visits to Monterey for the purpose of opening and preserving the eggs, and incidentally prepared a number of notes which are referred to in subsequent pages. Thanks to his care, about a dozen embryos of various stages were secured. There was still lacking, however, a series of segmentation and gastrulation stages, and to obtain these the writer paid a

second visit to the Californian coast during the summer of 1899. This visit resulted in the taking of 179 female Chimæra, from which 20 eggs were secured. In addition to the latter, a single egg containing a late embryo was obtained, which had become attached (65 fathoms) to one of the hooks of a trawl line. It is upon these stages, accordingly, that the writer has had to depend for his review of the development of Chimæra. He may add that he was able to secure several notes regarding the eggs of *Chimæra phantasma* and of *Chimæra mitsukurii* during a stay in Japan, and that he has further had the opportunity, thanks to his European colleagues, of examining Chimæroid eggs and young in several museums, notably in Paris, London, Berlin, Bergen, and Tromsoe.

The present introduction would be seriously incomplete without reference to the generous aid which has been given the writer at various stages of his work. Especially helpful were the suggestions of Dr. Tarleton H. Bean and President Jordan, and the many courtesies received from Professors Gilbert and Jenkins, Directors of the Hopkins Laboratory, and from other members of the staff of Leland Stanford University, notably Professor Wilbur. Grateful acknowledgment should be made to Professor Theodore N. Gill, who very generously examined the proof of the present paper. In Japan, also, while a guest of the Imperial University's laboratories, both at Tokyo and Misaki, the writer acknowledges the valued aid of Dean Mitsukuri and his associates. Finally, especial thanks are due to Dr. Naohide Yatsu, Rigakushi, for his assistance both in Japan and in New York, preparing many text-figures, and aiding notably in the section of the present memoir dealing with the fertilization of the egg. During the latter study Mr. Yatsu's comments, it need hardly be added, were especially valuable in view of similar studies which he had undertaken in the case of invertebrates.

The present memoir includes the following themes:

I. Chimæra and its characteristics. Appearance, movements, sexual differences, feeding.

II. Development:
- Breeding habits, mode of depositing eggs, and rate of embryonic development.
- The capsule and its formation.
- The egg and its membranes.
- Fertilization.
- Segmentation.
- Gastrulation.
- Early embryos, *i. e.*, prior to appearance of gill-openings.
- Late embryos, *i. e.*, from appearance of gill-openings to time of hatching.
- Immature young.
- Morphology. Reference to: (*a*) integument and dentition; (*b*) skeleton; (*c*) viscera; (*d*) nervous system.

III. Fossil Chimæroids and their significance in the study of recent forms.

IV. Chimæroids in the problem of vertebrate descent.

V. Literature of Chimæroids.

I. CHIMÆRA AND ITS CHARACTERISTICS.

THE LIVING FISH: COLOR, SIZE, DISTRIBUTION, HABITS.

This section was suggested as a beginning for the present memoir, since, in spite of many references, no observations have hitherto been published describing the living fish. In fact, the impression which the rank and file of zoologists have of Chimæra is, I believe, derived from the figure* given by Valenciennes in the illustrated edition of Cuvier's Regnè Animal, which has been copied trustfully by text-books, even by those which have appeared during recent years. This figure was evidently taken from a stuffed specimen, and gives the grotesque appearance of one of Aldrovandus's monsters, thus well meriting the name of "Chimæra." It is a sur-

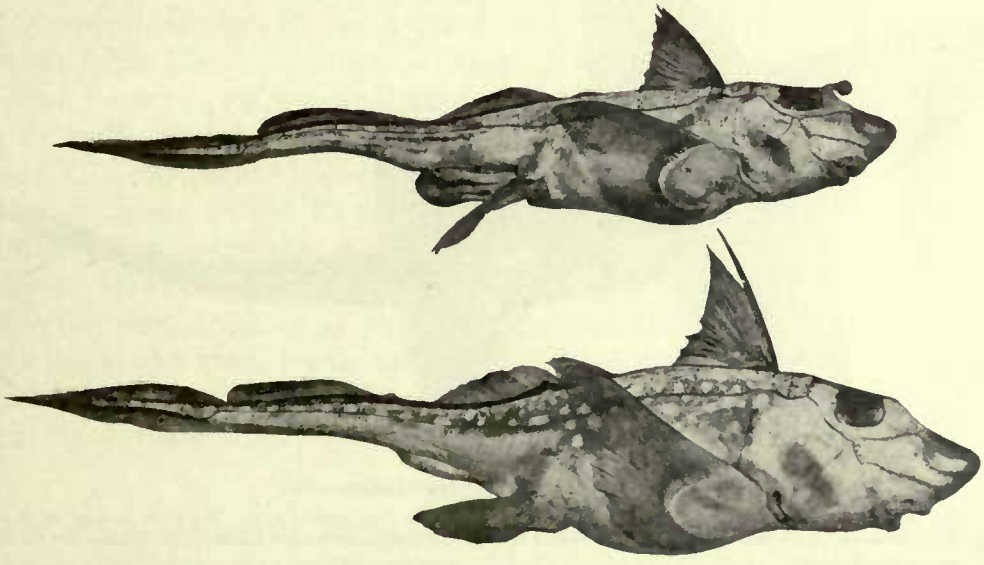


Fig. 1.—Chimæra colliei. One-fifth actual size.

The upper specimen, a male, shows the frontal clasping organ everted, a position which was only retained by fastening the organ in this position. The mixipterygia were turned somewhat sideways, so as to make them more apparent. The antero-ventral clasping organ is not conspicuous, but its tip is seen to protrude from the vertical slit immediately in front of the pelvic fin. The figure indicates the translucency of the snout region.

The lower, larger specimen, a well-grown female, shows immediately above the base of the ventral fin the tumid eminence at the opening of an oviduct. It illustrates, as secondary sexual characters, the narrower pectoral fin and first dorsal.

The photographs illustrate the translucency of the fins and delicate sheen of the newly-caught specimens.

prise, therefore, to find that the fish is, in point of fact, remarkably beautiful, its contours well rounded, its fins delicate, and its colors almost herring-like in brilliancy. Instead of "Chimæra" it deserves rather its popular Norwegian name, "king of the herrings," or, better still, its Japanese name, "gin-same" (silver shark). On the other hand, it can not be denied that there is a suspicion of grotesqueness

*This is scarcely more satisfactory than the "fantastic figures of Clusius and Aldrovandus," to which this author refers.

in Chimæra. In the water the moving fish gives one the impression that its pectoral fins are too large for its body; they stand out prominently, and from their transparency they remind one strongly of those of some specialized teleost, such as a gurnet or a flying-fish. In figures (figs. 1 and 2), reproduced from photographs, the transparency of the pectoral fins is indicated, though we gain little idea of their delicacy and beauty. They are well supplied with blood, which passes through the transparent fins in delicate vessels arranged parallel with the fin rays and sometimes gives the fin a rosy tinge.

COLORS.

Chimæra colliei, of which an immature specimen is pictured in plate XI, shows lustrous colors when taken from the water. Its ground tone is silver, but at every movement it reflects metallic hues—brass, copper, and gold. Its snout is trans-

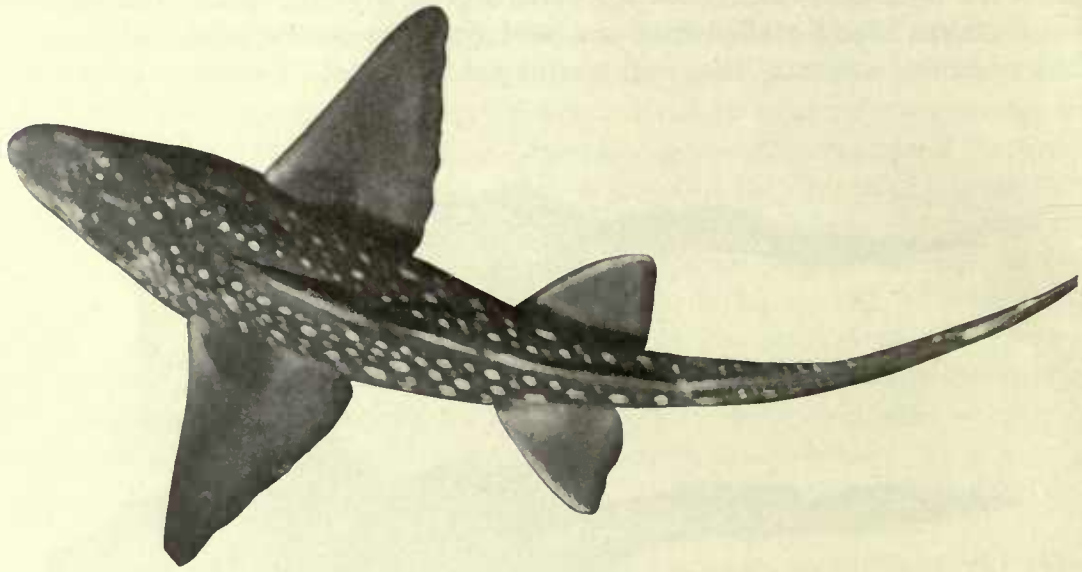


Fig. 2.—Photograph of living Chimæra colliei.

This shows the pectoral fins extended on either side of the body at the time of the down stroke of the fin. The pelvic fins stand out on either side apron-like, showing clearly their light-colored anterior border. In this position the spotting of the back is conspicuous. In lateral view (cf. fig. 1) the spots can scarcely be seen.

lucent, its optic cup is luminous, refracting pale greenish-blue, its iris brassy, and on head and trunk are tinges of rose, cobalt, pale-green, and madder. Out of water, however, its brilliant tones soon fade, and its delicate, scaleless skin blotches and dries. In the aquarium, as one could naturally expect, the fish fails to show much of its metallic luster, but, on the other hand, its pigments appear to greater advantage. Its back region is dark umber, through which pass, as the fish changes position, shades of olive and rose-madder. Its ventral region and fin bases are white, the fins themselves translucent and even transparent. In the adult the paired fins show little pigment; they stand out from the body prominently, their anterior rims white, and their constant movement adds greatly to the fish's beauty. It may be added that the dorsal spine shows brightly in the water, forming a

conspicuous anterior rim to the dorsal fin, whose remaining margin, in reality of a dark umber, now appears jet-black. In side view the body of the fish exhibits white spots, but they are not noticed in many positions. From above, however (fig. 2), they are conspicuous, and the general ground tone of the fish appears much darker, a change in coloration which is probably of value for protection.

In the matter of color *Chimæra colliei* is not far from the mean of recent Chimæroids; for some of these have but little pigment, while others are dusky and even black. This range in color might be expressed in somewhat the following way: With least pigment are the Callorhynchids, with clear silvery sides, obscured only by several large lateral blotches, and *Chimæra phantasma*, with silvery sides marked with longitudinal dark stripes. With increase of pigment come the series *C. monstrosa*, *C. affinis*,* *C. colliei*, *C. mitsukurii*, *C. purpurascens*, and *C. ogilbyi*, the last almost entirely black. The distinctly abyssal types, unshaded, uniformly plumbeous, with pigmented lateral line, are Rhinochimæra, Harriotta, and *C. plumbea*.

SIZE.

The general relations of size in Chimæroids will be referred to on a later page. The recent forms present a range of length from about 60 to 200 cm. *C. mitsukurii*, even including its long opisthure, is the smallest species, and the gradation in size extends somewhat as follows through the series: *C. colliei*, *C. affinis*, *C. monstrosa*, *C. ogilbyi*, and *C. phantasma;* and in the neighborhood of a meter in length are all other forms except *C. purpurascens*. Following the general rule among other fishes, males are smaller than females; in length less by about one-twelfth, and in weight by about one-seventh. In this connection a few comments may be added regarding the general shape of the fish. In Callorhynchids and in *C. phantasma* the modeling of the head, trunk, and tail is compact and suggests that of Cestraciont sharks. In general, males are more slender than females. This relation is shown in fig. 1, taken from a photograph of the freshly caught fish.

OCCURRENCE, HABITAT.

Chimæroids are widely distributed (*cf.* species list, pp. 6, 7). Callorhynchus, however, is limited to the south seas, and Chimæra largely to the north. The distribution of Chimæra is clearly the more general, for *C. vaillanti* occurs at Cape of Good Hope and *C. ogilbyi* in Australia. It is the general belief that all Chimæroids are obtained from deep water, since the majority of the species occur at a greater depth than the 100-fathom line, while some indeed are abyssal. It is stated, for example, that *C. monstrosa* occurs in water as deep as 1,000 fathoms, *C. affinis*† in depths from 200 to 1,300, Callorhynchus up to 600, Harriotta from 700 to 1,000, and Rhinochimæra at about 700. On the other hand, it must be admitted that *C. colliei* occurs in relatively shallow water. Dr. Bean records (Oceanic Ichthyology, p. 32) that "it swims at the surface," and states further that "there is no evidence

*It is probable that the *C. affinis* recorded from great depths represents a new species.

†*C. affinis* is the most abyssal of elasmobranchs.

that it descends to very considerable depths." The writer has taken it in water of less than 5 fathoms in Puget Sound, and he obtained a specimen caught from the Monterey wharf in water of about 3 fathoms. He also secured over a score of immature specimens (measuring about 30 cm.) from a single haul of a seine along a shore reach near Port Townsend, at a depth not greater than 2 fathoms. It is known, furthermore, that egg-cases of this species are plentiful in shallow water. *C. phantasma* and *C. ogilbyi* also occur in relatively shallow water, *i. e.*, respectively from 10 to 50 and from 22 to 150 fathoms. It appears, further, that Callorhynchus is sometimes taken in water of no great depth. (Thus Plate records having dredged off the coast of Chile an egg-capsule in water of 10 fathoms.) It follows, therefore, that in the matter of vertical distribution Chimæroids are not widely different from sharks.

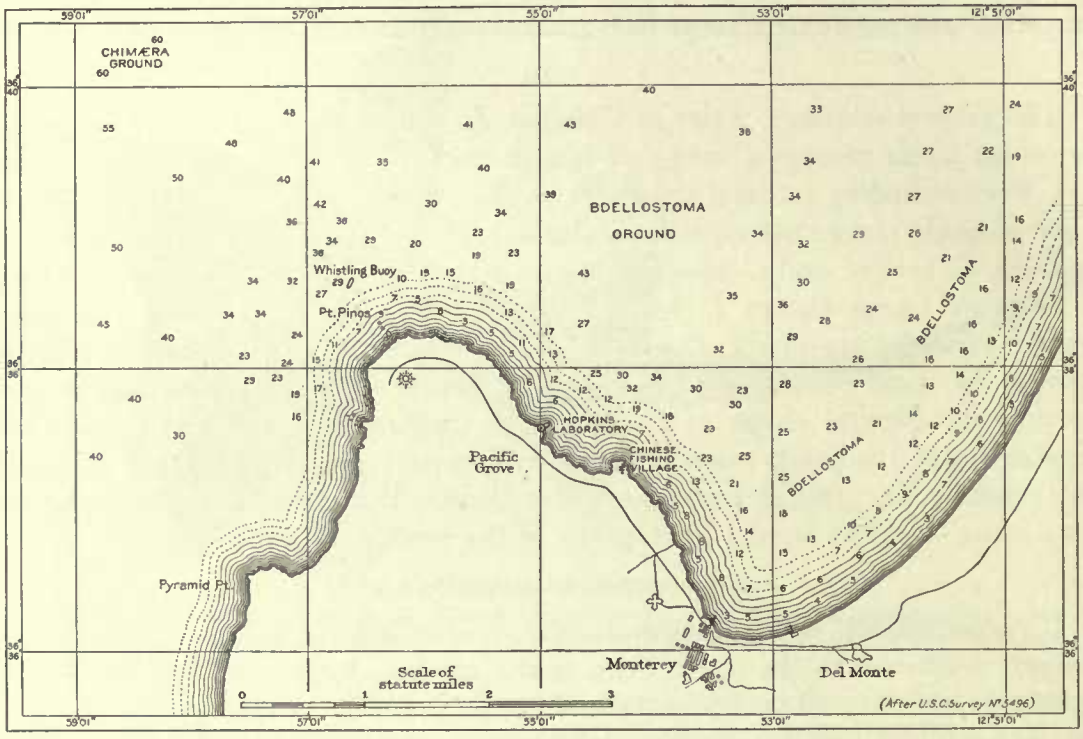


Fig. 3.—Sketch of the region of Monterey, Cal., showing the location of the fishing-ground for Chimæra.

Returning to the habitat of *C. colliei:* It can safely be said that this species is more abundant in shallow water in Puget Sound than at similar depths on the California coast—in this regard paralleling several other fishes as well as invertebrates. It is nevertheless true that in the region of Monterey specimens were often taken in water shallower than 15 fathoms; but experience demonstrated that the greatest number of individuals could be fished in water of 60 fathoms. It was also found that in somewhat deeper water, 60 to 120 fathoms, females, although less

abundant, were more apt to yield eggs, and that in water of less than 40 fathoms females were usually eggless. Collecting notes show that of 48 females taken in water shallower than 40 fathoms there was but a single specimen that yielded eggs, and in this instance the egg-capsules were quite immature. One concludes, accordingly, that near Monterey this Chimæroid occurs generally and at various depths, but that it is usually found at the time of spawning at a depth of somewhat over 60 fathoms. This conclusion is interestingly confirmed by the accidental taking of a naturally deposited egg-capsule on a hook of a trawl-line in water of 65 fathoms.

The best collecting-ground known to the writer is about 3 miles NNE. of Piños buoy, as indicated on the map (fig. 3). Here about 500 were taken, and it is to this region that the following notes apply. A trawl-line,* baited with squid or herring, can be laid in any direction with a reasonable prospect of securing fish; in fact, rarely less than 6 Chimæra are taken in a day's catch; on one memorable occasion 71 were taken. Tabulation of results shows that males are taken over five times as often as females,† and that of the latter (taken during the summer months) but 1 in 13 bears eggs which can be incubated. It is an interesting fact that in trawling the fish are often caught close together. The writer has seen as many as ten drawn into the boat attached to adjoining hooks. One infers from this that the line has fallen over a restricted feeding-ground, where the fish occur in great number. And it is found, furthermore, that if a fresh line is set over the same course more fish are usually forthcoming, and at the same stretch of the line. If, however, a line is set parallel to the first, and but about 200 feet distant, one is apt to find that no fish are taken. From the above observations one may naturally conclude that the especial feeding-grounds of Chimæra are sometimes small in size. Material brought up by the trawl-line indicates, further, that such a favorable feeding-ground is closely strewn with very small rock fragments. Where large rocks occur Chimæra is less common, and it is relatively rare on a sandy bottom. There is also evidence for the belief that Chimæra occurs in schools; and this view, it may be remarked, is prevalent among fisher-people in widely separate localities, as in Lisbon, Messina, Bergen, Monterey, and Misaki.

Chimæra is plentiful near Monterey. According to Ah Tack, however, an even more favorable fishing-ground occurs about 10 miles to the southward, near Point Lobos, and it is said to be well known to the Chinese fishermen of the neighboring Pescaderos. From this neighborhood eggs were collected during the winter season.

In the region of Monterey the temperature of the water during the summer months ranges between 50° and 60° F., and the specific gravity is about 1.028.

*Six or seven baskets (*i. e.*, lines) were usually set, having altogether about 5,000 hooks. The boat employed was a Chinese fishing skiff.

†This result agrees with the observations of Grieg and Olsson for *Chimæra monstrosa*. Costa, on the other hand, states that in the Gulf of Naples no less than 14 were females out of 16 specimens examined (between 1830 and 1851), and in Norwegian waters Malm notes that 26 out of 33 specimens were females.

MOVEMENTS.

Chimæra colliei is essentially a delicate fish. When taken from the water it struggles but little and soon dies (about 15 minutes). It makes no sound, save on rare occasions, when it clicks its dental plates together; and it shows no effort to erect its dorsal spine. In handling it the fishermen take less account of the formidable spine than of the jaws, which are capable of inflicting a painful wound, in one case snapping out at a single stroke a bit of skin and flesh. It is a difficult fish to keep alive, even under favorable conditions. In the aquarium of the Hopkins Station it lived rarely longer than two days.*

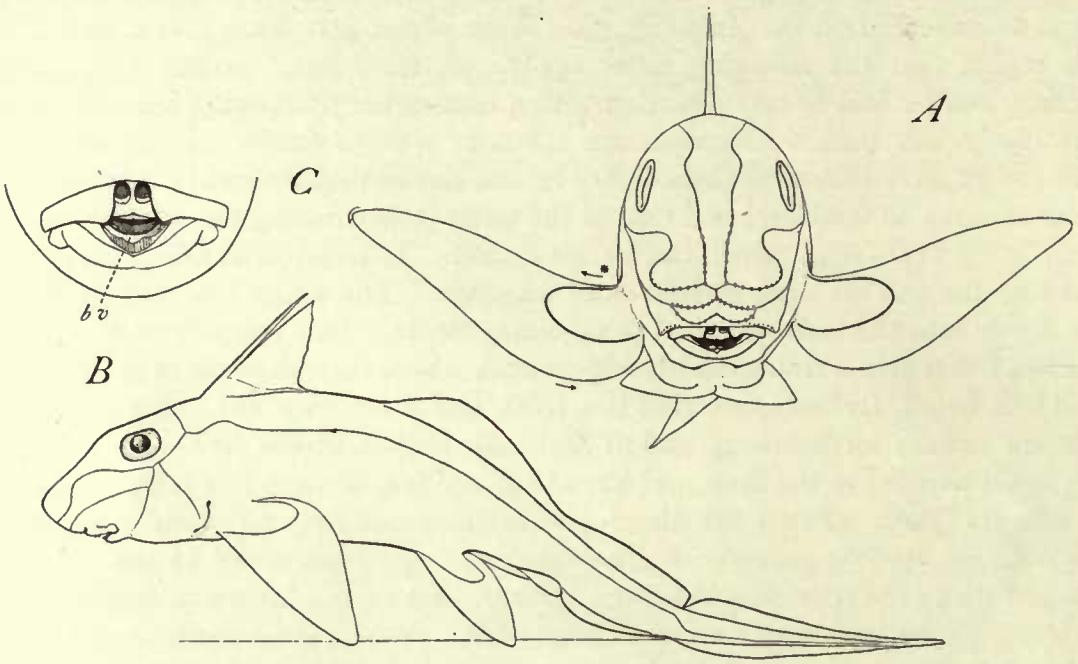


Fig. 4.—Chimæra colliei. Sketches of the living fish.

A. Swimming fish shown from in front. This indicates particularly the position of the pectoral fins; from the point marked with an asterisk (*) undulations arise which pass out over the tip of the fin as indicated by the arrows and end at the fin's posterior margin.

B. Fish shown in resting position. The tail droops somewhat and the weight of the trunk is apt to fall upon the fleshy pad which is present on the ventral side of the body immediately behind the mixipterygia. The opening of the operculum and the position of the mouth in this, as io the preceding figure, are iodicated in their normal position.

C. Mouth region, showing the extent to which the jaws open during the process of breathing. As here shown, the opening is even greater than usual. Behind the mandibular plates cao be seen the wide breathing valve *b v*, and the prominent anterior nostrils. The latter serve to pass water lateralward under the large labial folds into the mouth.

The moving fish is conspicuous in the use of its paired fins. The pectorals are in constant motion, like delicate translucent fans† moving to and from the body, and passing undulations one after another along their delicate rims, somewhat as in the pectorals of skates. Thus, in the sketch given in fig. 4 A, these fins are seen in a characteristic position. They are supposed to be moving dorso-ventrad, the path of their flexible tips describing an arc of about 90°. At the ventralmost

*Mr. C. F. Holder, the director of the aquarium at Avalon, Santa Catalina Islands, informs the writer that he has been able to keep *C. colliei* alive for a longer time, although no definite time was recalled.

†The translucency of the pectoral fins is seen in the photograph reproduced in fig. 1, page 11.

point of their movement they appear in the position shown in fig. 4 B. A large part of the movement takes place in the dermal web of the fin. Starting from the point marked with an asterisk (*) a wave of movement passes out to the apex of the fin, where its greatest height is shown; then it passes rapidly around the ventral rim and dies out in the axil. This wave is followed by another, more or less rapidly, according to the effort of the fish. As the dermal rays are parallel to one another, their fall and rise suggest the movement of the keys of a piano when a finger is drawn across the keyboard. As so much of the conspicuous movement is accomplished by dermal rays, the muscular bases of the fins show to full advantage as balancing organs (*cf.* fig. 2), almost as in Polypterus. It may be mentioned, in connection with this constant movement, that the dermal margin of the fin is so delicate that it soon becomes ragged by wearing against the sides and bottom of the tank.

Chimæra is deliberate in its general movements, suggesting somewhat a shark, but occasionally it shows great activity. On one occasion a fish which had been balancing quietly for some minutes suddenly dashed about the aquarium and then shot up over the side. Quick movements of the pectoral fins greatly aid the fish's forward propulsion; and in the undulation of the body the dorsals are far more important as swimming organs than the caudal. The ventrals serve rather passively as balancing organs, preserving a horizontal plane and hanging behind like an apron, their median edges overlapping (fig. 4 A). It may be noted that the mixipterygia, which are so conspicuous a feature in museum specimens, are hardly seen in the swimming fish (fig. 4 B). They are neatly tucked together behind the ventral fins in the median line and can little impede movement. In slow forward movement Chimæra rocks somewhat from side to side, the dorsal fin functioning imperfectly as a keel, its spine, by the way, rarely more erect than shown in the figure. In resting the tail droops noticeably* and the fish balances by slow movements of the pectorals. The hinder trunk sometimes rests on the prominent pad of the postanal region. (Pl. 1, fig. 2, *c*.)

In further detail: The fish sometimes swims about freely, with a movement described by an observer as "butterfly-like," from the conspicuous flapping of its large pectoral fins. It is more active at night; if placed in a large tank it is apt to swim restlessly from one end of the tank to the other. In daytime it is quieter, and appears to avoid strong light. Occasionally it "sails" or "flutters" to the surface, thrusts its snout out of water, and then, suspending all movements, sinks to the bottom. Here it sometimes rests, balanced on the tips of its fins, like a dipnoan, or Squatina, or even a ray. In this position, when otherwise quiet, its brilliant eyes often show active movements. One receives the impression that captivity is irksome to the fish, an impression often strengthened by its subsequent behavior, for it will suddenly advance, then retreat, advance again, and sometimes thrust itself out of the water in its attempt to escape.

*This condition has been recorded in weak, aquarium-bred fishes (*e. g.*, Lepidosteus), but in Chimæra it is probably normal, since it was observed in freshly caught specimens. There is, nevertheless, the possibility of its being due to change of pressure.

The mode of breathing of the fish is somewhat remarkable. The mouth is very small, and its rims are motionless or almost motionless, scarcely parted in breathing; so nearly closed, in fact, that the movement of the breathing-valve can hardly be seen. A portion, probably a large portion, of the water—as in the case also of dipnoans—is breathed through the prominent nasal openings (fig. 4 A and C), whose cartilaginous marginal flap is specialized to this end; and since the mouth is motionless, it follows that the branchio-opercular muscles are the efficient means of introducing water to the gills. In point of fact, in the living fish one readily observes an extensive dilation and contraction of the opercular flaps. In spite, however, of this extensive movement, the excurrent opening is remarkably small, and at this point the opercular fold puffs out conspicuously, like an opened valve, a small one at that, forming a slit about three-sixteenths of an inch in diameter. The rhythmic opening and closing of this slit gives a further suggestion of its valvular nature. The breathing, moreover, as in the case of other fishes, is rendered more effective by the presence of oral breathing-valves, operating so as to close not merely the opening of the mouth, but the nasal passage also. The respiratory movements are rapid, at least in captive fish. In such specimens there are counted as many as 100 respirations a minute, a number evidently abnormal. Occasionally, when the fish is swimming, the mouth will open two or three times spasmodically. This occurs too rarely, however, to be of especial respiratory value; and it is also to be observed, if the fish is a male, that the frontal clasping spine will at the same time be elevated and depressed.

This correlated movement of clasping spine and jaw has already been suggested by Reis on anatomical grounds. In this connection it was once observed that both mixipterygia were suddenly dropped from their position close to the trunk, rotating downward together from their bases, their tips rotating through an arc of 90°, just as rigid fingers might be bent downward from the plane of the hand, but no details of this process were seen, for they at once rotated backward into their closed position.

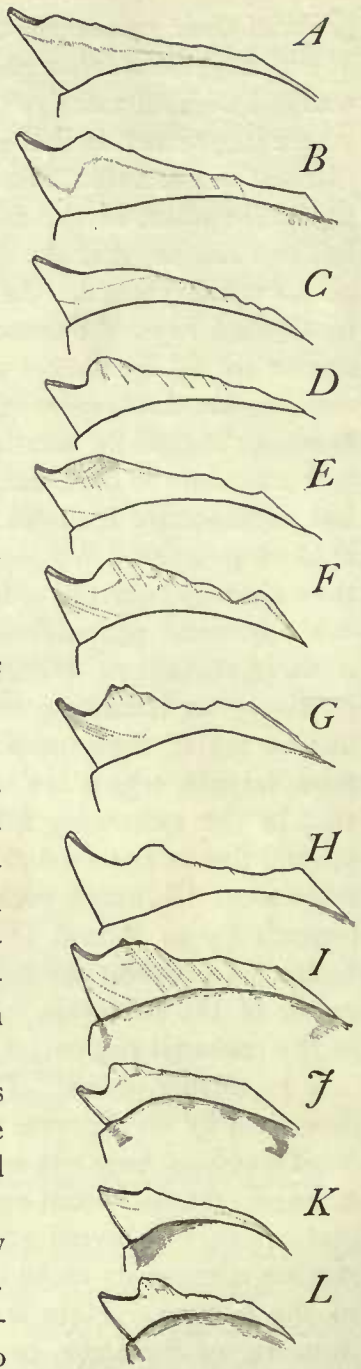


Fig. 5.—Mandibular dental plates of Chimæra colliei, shown in outer lateral aspect, and indicating variation in these structures. A–I, specimens from females; J–L, from males.

SEXUAL DIFFERENCES.

In living specimens it is surprisingly difficult to distinguish the sexes (*C. colliei*). The secondary sexual characters of the male are then inconspicuous, and one is apt to identify it rather by its smaller size and by its slightly darker tone. Breeding colors are not marked, but at the time of spawning the female shows considerable color in the anal and caudal regions, the fins especially being suffused with blood. In males, those, it appears, are in breeding colors in which the anterior rim of the pelvic fins and the anterior region of the pectoral fins are the whitest. It is difficult to distinguish the claspers. The frontal organ is folded neatly away below the surface of the head; the mixipterygia are closely apposed to the trunk, hardly modifying the contour of this region; the anteropelvic claspers are tucked into their dermal pouch, and the mouth of the pouch is nearly closed. In the female a fleshy pad lies in the median ventral line behind the pelvic fins, and produces a contour not unlike that of the combined mixipterygia. Closer examination shows slight differences in the proportions of male and female; thus (*cf.* fig. 1) in the male the eye is relatively of larger size, the snout more obtuse, the fins shorter and wider, the dental plates smaller and often distinguishable in shape.

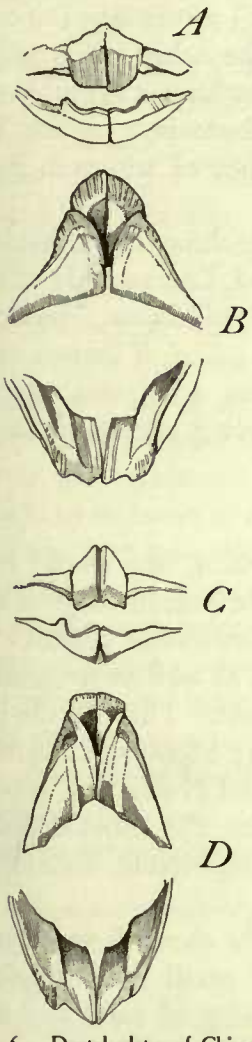


Fig. 6.—Dental plates of Chimæra colliei.

A, front view of dental plates of large specimen (female).

B, dental plates of same specimen, viewed in visceral aspect.

C, front view of dental plates of male. Observe especially the asymmetry of the right mandibular plate.

D, dental plates of same specimen, viewed in visceral aspect.

Dental plates.—In *C. colliei* the mandibular dental plates of the female do not usually exhibit as marked a prong in the "canine" region as the males. Nine such plates are shown in fig. 5 A–I, sketched from jaws of adult females selected at random, and these may be contrasted with the common type of the mandibular plate of the male outlined in fig. 5 J and L. Great variation is, however, apparent in both cases. Of the nine plates figured, four (A, C, E, I) have no conspicuous "canine" prong, two have the prong well marked (D, C), the rest are intermediate. In the males seven plates out of ten were found to be conspicuous in the "canine" prong, quite similar to the specimen figured (J, L). One specimen (K) only was remarkable for the evenness of its edge. Variation was also marked in the number, arrangement, and distinctness of the tritors, and in the general thickness of the dental plates. These characters, however, are partly dependent upon the age of the fish. In the young the plates are more delicate and regular, and when viewed against the light they are less apt to show tritoral lines. When the latter appear they are slender and translucent. In large specimens

the plates are stouter and show irregularly worn margins. In somewhat rare cases asymmetry results. Two instances of this kind are shown in fig. 6. In the first (A and B) the upper "incisor" plates are quite different in shape (a female); in the second (a male, C and D) the mandibular plates are irregular, one having the typical "canine" prong, the other a fairly straight margin. In visceral aspect one (D) carries the median tritors of the palatine plates far forward; the other (B) is practically without a median tritor. In one (D) the mandibular plates form a symphyseal beak-like prominence; in the symphysis of the other (B) there is a noticeable notch. In general, there is considerable variation in the number of tritors in individuals of apparently the same age.

The foregoing peculiarities are commented upon, since they show that considerable judgment is necessary to determine accurately species of Chimæroids when dental plates alone can be studied, *e. g.*, in the case of many fossil forms. Indeed, with so wide a range of variation, it is quite conceivable that *C. colliei*, if known only by its dental plates, might be described under several species, and possibly two genera. The general relations of the dental plates in both living and fossil forms are considered on a later page.

FEEDING AND FOOD.

In view of the special character of the dentition of Chimæra, one would naturally expect its food supply to be definite in character. The examination of the contents of its gut, however, showed (*C. colliei*) singularly omnivorous habits. It is true that the broken shells of mollusks are commonly found, as well as fragments of good-sized crustaceans, as indeed the scanty literature records. Thus, in the gut of *C. monstrosa* Faber finds crustacean and shell-fish fragments; Monticelli, quoting Lütken, *Cyprina islandica;* and Olsson, broken shells (*Leda* and *Venus*) and bits of large decapods. Olsson finds also (and his observations are the most detailed hitherto published on the feeding of Chimæra) chætopods, amphipods, echinoids, and polyps.

In *C. colliei* observations on about a score of individuals showed a singular mixture of foods. Most numerous were vertebral columns of small isospondylous fishes, a few mollusk shells, usually greatly crushed, a quantity of sand and fine gravel, squid, nudibranchs and opisthobranchs, bits of cases, jaws, and setæ of annelids, and occasionally a fragment of a crustacean. In one instance the gut was filled with seaweed. One is not surprised, therefore, that this species is taken readily with various baits. In Puget Sound it is fished with mussel, clam, prawn, sandworms, and even salt pork. At Monterey the greatest numbers were taken with squid; failing this, trawls were baited with herring, fresh or salted.

A curious feature in connection with the feeding conditions of Chimæra is that in so many specimens examined the gut is found entirely empty, even at the time the fish is taken from the water. This condition has been commented upon by several authors, among others by P. J. Van Beneden and Olsson, the latter finding

the gut empty in as many as 5 examples out of 16. The explanation of this is, however, we believe, not necessarily due to cessation of feeding, for it is found that the fish does not cease to feed even while in the act of depositing eggs. On the other hand, from the simplicity of the valve of the gut* it is quite probable, as experiments on living fish have convinced the writer, that the food material is voided between the times of hooking the fish and of drawing it into the boat.

Another curious feature connected with feeding is that Chimæra, in spite of the small size of its mouth, can ingest objects of large size. Thus it was found that a specimen of *C. colliei* of moderate size, one whose mouth appeared too small to admit a finger tip, had ingested a fish 6 or 7 inches in length. Whether it had swallowed it in a single piece is doubtful, but judging from a section of vertebral column, a fragment 2 or 3 inches long had been taken. Another specimen had swallowed a portion of a crab's carapace nearly an inch in length. Indeed, the usual baits taken measure over an inch in diameter, and it is found that they are easily bolted, not cut or crushed by the dental plates. No observations are recorded as to the way in which the small and delicately shaped mouth behaves while feeding. As far as the experience of the writer goes, a fish will not feed in captivity, and it can rarely be induced to notice a bait. In one instance the mouth opened rather widely and the jaws snapped together with an audible click. It was evident, however, even from a single observation, that the mouth is accurately adjusted and can focus its stroke with precision, somewhat after the fashion of the beak of a bird; and there can be no doubt that the dental plates of this species form together a powerful instrument for cutting, rather than crushing. On one occasion the writer saw them part the line of a trawl.

In spite of formidable dentition and erectile dorsal spine, Chimæra is preyed upon by other fish. According to Olsson it is eaten by *Somniosus microcephalus*, and small specimens have been found in the stomach contents of cod.

*The stomach is broadly continuous with the intestine; when food is found it usually occurs in the first turn of the intestinal valve.

II. DEVELOPMENT.

BREEDING HABITS.

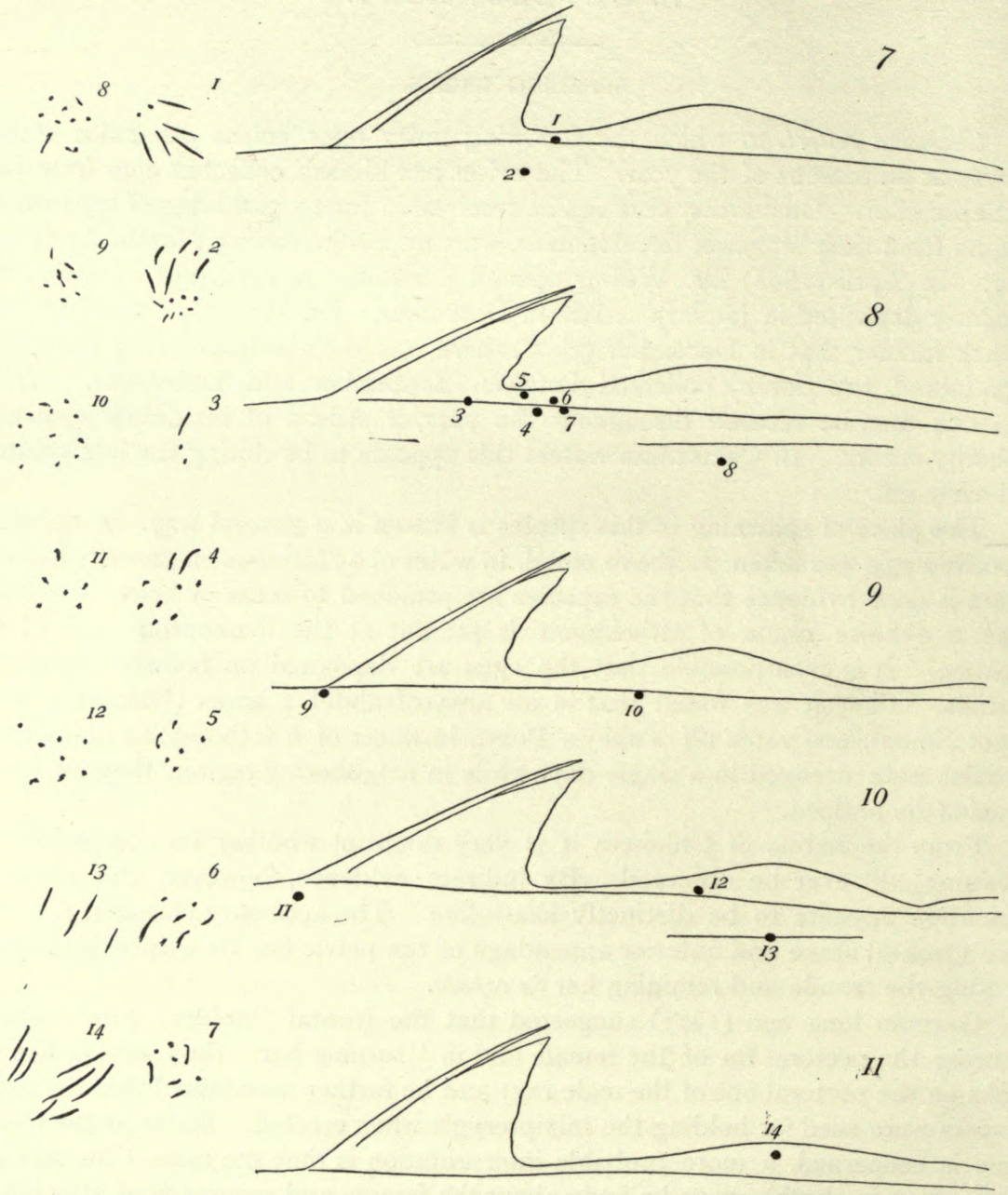
Chimæra colliei, to which the following notes refer unless otherwise stated, spawns at all seasons of the year. The writer has himself collected eggs from June till September. On another occasion he received in June a gathering of eggs which, judging from their stages of development, were deposited during March, April, and May. In April (1898) Dr. Wilbur opened a number of eggs, one of which was evidently deposited in January or late in December. Dr. Wilbur's collecting notes remark further that in December (1898) there was lost a hatching-case containing eggs (about two dozen) collected between September and December. While eggs can thus be secured throughout the year, a season of maximum spawning probably occurs. In Californian waters this appears to be during the late summer and early fall.

The place of spawning in this species is known in a general way. A naturally deposited egg was taken, as above noted, in water of 65 fathoms on gravelly bottom. There is good evidence that the capsules are attached to rocks or heavy sea-weed, since a definite organ of attachment is present at the filamentous end of the egg-case. It is even possible that the eggs are deposited on favorite spawning-grounds. Thus it was found that in an area of about 2 acres (Discovery Bay, Puget Sound, 200 yards off Tukey's Point, in water of 6 fathoms) as many as 85 capsules were dredged in a single day, while in neighboring regions they were only occasionally noticed.

From the habits of Chimæra it is very doubtful whether its copulation and spawning will ever be observed. By indirect evidence, however, the mode of copulation appears to be distinctly shark-like. The accessory claspers, *i. e.*, the male's frontal spine and anterior appendage of the pelvic fin, are evidently of use in securing the female and retaining her *in copulo*.

Garman long ago (1877) suggested that the frontal "holder" functioned in securing the pectoral fin of the female and in "turning her," thus serving like the hooks on the pectoral fins of the male ray; and he further maintained that the pelvic claspers were used for holding the mixipterygia when erected. As far as the frontal spine is concerned, a more probable interpretation is that the male Chimæra (*cf.* the position in shark) wraps its body about the female and secures final attachment *in copulo* by attaching the spine near the female's dorsal fin; for it was found, in an examination of specimens which were about to deposit eggs, that well-marked scars were present, indicating the point of attachment. The region of the dorsal fin in such examples is shown in figs. 7 to 11; and there can be no question, from a closer examination of the scars, each of which is shown enlarged on the same page

according to corresponding numbers, that these were caused by the frontal organ, for each shows a number of small punctures, usually 8 to 12, corresponding in arrangement to the cusps of the frontal spine, as one may demonstrate by experi-



Figs. 7 to 11.—Region of dorsal fin in female specimens of Chimæra colliei, showing marks of frontal clasping organ of male. The smaller numbers, 1 to 14, and (at the left) enlargements with corresponding numbers, show positions and details of scars made by frontal clasping organ.

ments with the spine itself. The majority of these scars occur, moreover, in the position where they would be expected if the male assumed *in copulo* the same position as the shark. With few exceptions they are situated in the region of the

first dorsal fin. In some instances the presence of several scars indicates that a number of attachments were attempted. The most posterior scars (figs. 10 and 11, scars 13 and 14) are rather scratches than points of attachment. In spite of this evidence, however, the writer must remark that one gravid specimen examined failed to show a scar in the region referred to. On the other hand, there was little doubt that the marks referred to were made on the fish prior to capture, and that in those specimens no other marks were noticeable.

The antero-pelvic clasping organs are distinctly erectile and probably serve as an additional means of attachment *in copulo*. They can hardly function as Garman has indicated (*i. e.*, to hold the erected mixipterygia), if for no other reason than that if thus held the mixipterygia not only diverge widely, but are so closely fastened to the side of the male that they can not well be made to enter an oviducal opening.

It may be noted that Parker (1897) states that spermatophores are present in Callorhynchus.*

MODE OF DEPOSITING EGGS.

Two eggs are deposited almost simultaneously; and it is more than probable that, just as in sharks, considerable time is taken in the actual process of extruding the eggs. In fig. 12 is shown the anal region of a specimen (*C. phantasma*) in which the egg-capsules were protruding. This specimen, it may be said, had been rather carelessly handled and had been in the well of a fishing-boat nearly half a day, but the eggs showed no tendency to become detached. The capsules in this instance are still deeply inserted in the oviducts; even at a later stage they remain firmly attached. In the condition shown in plate 1, fig. 4, the capsules protruded as far as the base of their terminal filament, yet they remained attached to the fish for several hours and were thus brought to the Hopkins laboratory. It was then found, as the figure indicates, that the terminal filament passed throughout the length of the thickened portion of the oviduct and terminated in an expanded tract in the crease at the lower end of the capsular gland. At this stage the walls of the lower oviducts were contracted and embraced tightly the capsular filament. At a still later stage the filament hardens into a dark-colored string, and the capsules then hang freely into the water, 2 or 3 inches distant from the body.† Such a condition was once observed by the writer, and he found that even thus the eggs were firmly attached. In removing them the connecting strings were observed to possess considerable elasticity. They could even be lengthened and shortened several inches. When detached from the fish they showed that the terminal was still immature, soft, and pale in color. It is to be regretted that in this specimen no dissection of

*Doubt has been expressed as to the presence of a *receptaculum seminis*. (Hyrtl in Sb. Akad., Wien, 1853, XI, pp. 1078–1087, and Redecke, Tydschr. d. nederl. Dierkund. Ver, 2d ser., Decl. VI, 1899, p. 125.) In this connection *cf.* Howes as to a "rudimental vesicula seminis" in Chimæra (♀). (J. Linn. Soc., vol. XXIII, p. 405.)

†Prof. Einar Lönnberg, in a recent letter, which I am permitted to quote, states that he has observed (in July, 1898, in the market of Bergen), a specimen of *Chimæra monstrosa* in which egg-capsules were protruding from the oviducts, somewhat in the condition shown in the present fig. 12.

the oviducts was made, for the filaments were so perfectly formed that they might well have yielded some interesting notes as to their terminal. That this is finally a bulbous organ there can now be no doubt. Ah Tack early made a drawing of it, but the writer's skepticism* continued until word was received from Dr. Wilbur (May 1, 1899) that he had himself seen the terminal organ, describing it as a "sort of disc," and figuring it (plate 1, fig. 3) very much as Ah Tack had done.† From all this it follows that the ovulation of this Chimæroid is highly specialized. The elaborate egg-case is not shot out quickly nor festooned on fixed objects by its terminal filament, as in the case of recent selachians, but is carried

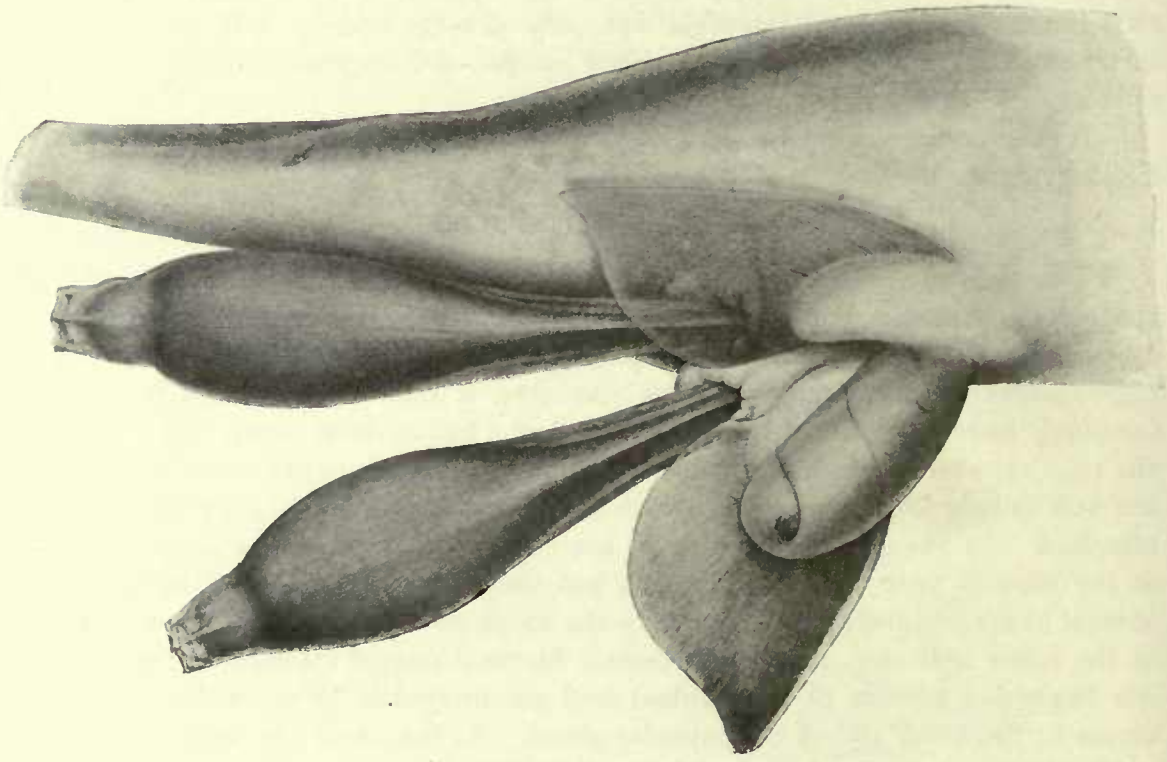


Fig. 12.—Region of ventral fins of a specimen of Chimæra phantasma, in which egg-capsules protruded from oviducts. This specimen was taken (Misaki, Japan) in water of about 150 fathoms and shows the intestine everted, a condition usual in a fish taken from such a depth.

about for a longer time, protruding from the oviducts before it is made fast to a suitable object. This is possibly a stone,‡ and if the eggs are thus attached near or among rock masses, we have a suggestion why embryo-bearing capsules have never been dredged.

*Pains were taken to observe the process of depositing the eggs. To this end a fish was secured in which egg-capsules were just protruding. This specimen was closely watched, but succeeded, nevertheless, in depositing the eggs unobserved. The process could not have taken more than 10 minutes. The capsules were immature, possessing scarcely more than a stump of the filament (plate 11, fig. 10).

†Unfortunately this capsule was lost in a hatching-case swept away by a storm.

‡Ah Tack states that several times his trawl lines have brought to the surface capsules which still retained small stones attached to the terminal organ of the filament.

It is observed that after the eggs are deposited the oviducal openings are everted, tumid, suffused with blood (plate I, fig. 2; *cf.* also Costa, p. 23, plate II, and Gaimard, plate XX, in Voy. en Islande et au Groenland); in fact, the entire anal region is bloodshot, including the fin margins.

In many instances (August and September) the fish may soon spawn again. This is evident from the mature condition of a pair of ovarian eggs which were found in specimens having tumid oviducal openings.

RATE OF EMBRYONIC DEVELOPMENT.

The young Chimæra spends the greater part of a year in its capsule, probably not less than nine months, and possibly as long as twelve. The duration of the younger stages is known with reasonable accuracy. In the following table, showing the rate of development of *C. colliei*, the results are based upon eggs in hatching-cases (water temperature between 50° and 60° F.).

TABLE B.—*Rate of Embryonic Development.*

Stage.	Estimated duration of entire process.	Approximate age of specimen in material studied, time of fertilization included.*
Fertilization...	36 to 60 hours.	
Cleavage....	3 days.	
First.....	.....	2 days 3 hours.
Second...	.....	2 days 5 hours.
Sixth.....	.....	3 days.
Blastula	4 days.....	5 to 9 days.
Gastrula	14 days.....	10 days.
		12 days, corresponding to Balfour's shark embryo stage C.
		19 days, corresponding to Balfour's shark embryo stage D.
		21 days, corresponding to Balfour's shark embryo stage E.
		24 days, corresponding to Balfour's shark embryo stage F.
Embryo.....	.....	28 days, corresponding to Balfour's shark embryo stage G.
		33 days, corresponding to Balfour's shark embryo stage I.
		90 days,† corresponding to Balfour's shark embryo stage L.
		130 days,† corresponding to Balfour's shark embryo stage N.
		180 days,† corresponding to Balfour's shark embryo stage O.

*A re-examination of the writer's collecting notes leads him to estimate that fertilization takes place in about two days. This time has therefore been added in assigning ages to the various stages.

†These figures are based upon notes given by the fisherman Ah Tack, recording months when eggs were placed in the hatching-cases. If these are accurate, and I believe they are reasonably so, Chimæra does not differ notably from a shark in its rate of later embryonic growth.

THE EGG.

The egg of *C. colliei* measures in its capsule about 2.9 by 1.9 by 1.3 cm. (average). It is inclosed in a delicate vitellina; when this is ruptured, the egg breaks into a syrupy mass, very much as the egg of a typical selachian. Especially soft is the egg about the time of its passage into the oviduct. At such a stage

(plate II, fig. 5), if placed on a flat surface, it spreads out circularly, measuring in this way over 5 cm. in diameter. It is pinkish (it is earlier yellow, and later creamy white), although its tint is probably due to the capillaries in the enveloping membrane. These capillaries, it may be noted in passing, become focused around a well-marked stigma.

In the disposition of yolk the egg differs slightly from that of typical selachians (*e. g.*, as shown by Rückert in Torpedo). (*Cf.* p. 47.) In the matter of fertilization, sperms have been found in the uppermost portion of the oviduct, and there can be little question that the earliest stages of fertilization here take place. It is further evident that the eggs are received in the oviducts one after another, for there is but a single funnel present, and it is probable, from the condition of the ovaries examined, that the eggs are shed from both right and left sides at almost the same time. By this inference we can also best explain the passage of the eggs, one to the right oviduct and one to the left, since if the first egg were blocking the upper portion of one oviduct, the second egg would naturally pass to the other. The fluidity of the egg at this stage unquestionably aids it in passing through the narrow opening of the oviduct in the zone of the capsular gland (plate II, fig. 6), granting even that this opening is greatly enlarged at the time of the egg's descent.

Fig. 13.—Spirangium (egg-capsule of Chimæroid?). From lithographic stone of Lerida (Spain). Jurassic. After Sauvage.

THE EGG-CAPSULE.

The egg-capsules of Chimæroids* are illustrated in figs. 13-23, and a list of those hitherto described, together with notes as to the depth at which they were collected, is given in Table C on page 29.

An examination of the capsules indicates that they may be grouped according to the genera and species which they repre-

*In the instance of *C. collici*, the parts of the young fish are found to have a definite relation to the egg-capsule, and these relations are probably constant in other Chimæroids. The capsule may therefore be referred to as containing a *case* for the embryo, which is always subdivided into *snout sheath*, *trunk sheath*, and *tail sheath*. The case has also a dorsal side, which bears anteriorly an opercular flap, which provides for the ultimate escape of the young, and a ventral side, which is (usually) the more convex. Other descriptive terms are: *Lateral webs*, which are flanges of the capsule extending outward from the *case*. These are sometimes strengthened transversely by stout undulating thickenings, *rugæ*, of the web; and these often pass over into, or are associated with, more delicate and more numerous distal *rugulæ*, or both rugæ and rugulæ may become close-set, rib-like thickenings passing from case to web margin, *costæ*; these terms will be found useful in description. *Opercular ridges*, overlapping, form together the rims of the opercular flap. In their specialization these rims have sometimes protruding *serrulæ*, which interlock and form a close-set grating, which admits water for the respiration of the embryo and which later breaks open to permit the young fish to escape from the capsule. These grating-like fenestrulæ are collectively homologous with the (pair or several pairs of) lateral slits which appear near the rims of the egg-capsule of the shark or ray. Continuing the line of the fenestrulæ, ventilating apertures are also present at the sides of the tail-sheath, and these may be termed *caudal pores*. They are typically furnished with "tongue-bars," which double the number of simple openings. A dorsal keel is present in the capsules of Chimæra.

sent. In further detail, the capsules may be classified on somewhat the basis shown by Table E on page 30. (*Cf.* this table for proportional measurements.)

TABLE C.—*Egg-Capsules of Chimæroids.*

Approximate depth at which deposited.	Species.	Reference. (For detailed reference *cf.* Literature List.)
Fathoms.		
10+	Callorhynchus*.....	1842 Müller, J.
		1865 Duméril, A
		1871 Cunningham, R. O.
		1880 Günther, A.
		1897 Parker and Haswell.
		1899 Garman, S.
		1901 Vavra.
		1901 Jaekel, O.
5 to 65	Chimæra colliei.....	1903 Dean, Bashford.
?300	mitsukurii	1904 Dean, Bashford.
?200	monstrosa	1855 Nilsson, S.
		1858 Lütken, C. F.
		1874 Collett, R.
		1877 Malm, A. W.
		1889 Günther, A.
		1892 Alcock, A. (C. monstrosa ?).
		1896 and 1899 Grieg, J. A.
		1896 Olsson, P.
		1901 Jaekel, O.
	phantasma.....	1889 Günther, A.
150		1904 Dean, Bashford.
375	Harriotta raleighana	(v. infra)
300–600	Rhinochimæra pacifica.....	1904 Dean, Bashford.
561	indica	1891 Wood Mason, J., and Alcock, A.

*Reference is made in the present paper (pp. 30, *et seq.* and figs. 15 B–F) to several "species" of capsules of *Callorhynchus; e. g.*, Specimen 7983, Zool. Mus. Jardin des Plantes, Cape of Good Hope (Quoy and Gaimard); Specimen 7982, Zool. Mus. Jardin des Plantes, Cape of Good Hope (Voyage Péron); Specimen 7984, Zool. Mus. Jardin des Plantes, Chile (Martinez); Specimen 8823 A, Zool. Mus. Jardin des Plantes, Straits of Magellan (Savatier). Also to specimens from Australia in the British Museum.

TABLE D.—*Egg-Capsules of Fossil Chimæroids.*

Ischyodus (= *Aletodus*) *ferrugineus:*
(Upper Jurassic) 1901, Jaekel, O.
The fossils Spirangium, Palæoxyris, Fayolia, and similar forms may prove to be the egg-capsules of Chimæroids or of cestraciont sharks. From their imperfect preservation, however, they may equally well be coprolites of fishes having spiral intestinal valves. To a somewhat more definite category, however, belongs the following "Spirangium":
Spirangium:
1903, Sauvage, H. E.
Cf. fig. 13. If this prove to be a Chimæroid egg-capsule it is remarkable in a feature suggesting the capsule of a cestraciont—marginal webs arranged in spiral.

TABLE E.—*Egg-Cases of Chimæroids Compared.* (*Cf.* figs. 13–16.)

Length (cm.).	Genus and species.	Percentage of breadth to length.*		Percentage of length of tail sheath to entire length.	Proportional length of opening valve from hinge to anterior end of capsule, *i. e.*, in percentage of total length of capsule.	Number of respiratory perforations along each side of opercular valve.	Number of respiratory (couples of) openings in caudal sheath.	Proportional length of rim of operculum bearing serrations (actual), *i. e.*, in percentage of total length of capsule.	Rugæ, number of.	Rugulæ, approximate number.	Costæ, number of.
		Breadth of trunk sheath only.	Entire breadth.								
14	*Spirangium*	17	36	----	----------	----------	----------	----------	----	----------	----
18	*Ischyodus* = *Aletodus.*	17	40	37	36	? Single slit on each side	? Single slit	(None)	12	38	----
	Callorhynchus.										
17	Jaekel's	16	45	30	36	Slit on each side.	Slit on each side.	----------	20	58	----
21	Duméril's†	13	29	31	35	----do----	----do----	----------	20	?	----
23	British Museum's	18	47	34	34	----do----	----do----	----------	12	7	----
?30	Garman's	----	19	56	?25	----do----	----do----	----------	8	62	----
24	Müller's	16	38	38	35	----do----	----do----	----------	12	37	----
28	7983 Jardin des Plantes. Fig. 15B	16	36	36	32	----do----	----do----	----------	17	55	----
32	7982 Jardin des Plantes. Fig. 15C	14	33	44	33	----do----	----do----	----------	14	55	----
22	7984 Jardin des Plantes. Fig. 15D	16	37	32	33	----do----	----do----	----------	16	51	----
24	8823 A Jardin des Plantes.	15	36	32	38	----do----	----do----	----------	16	39	----
	Chimæra.										
15–17	colliei	14–17	18	43	37	86 (+ many (30) rudimentary pores).	89	10 beginning in front.	35	----------	----
17	monstrosa	17	15	54	16	50 (very small).	75	6 beginning in front.	---	----------	----
27	phantasma	26	12	63	18	54 (+20 rudimentary pores).	62	5½ beginning in front.	5	100+ (absent in hinder ⅓ of length).	----
22	mitsukurii	22	12	56	?70	24	200+	5+ beginning in front.	----	----------	----
	? *Harriotta.*										
15	? raleighana	18	37	39	31	70+ beginning low and faint.	110	11 posterior in position.	----	----------	50
16	indica	15	32	38	18	?	185	?	----	----------	70
	Rhinochimæra.										
26	pacifica	13	3	32	35	48 low and faint.	45	12 posterior in position.	----	----------	56

* As the filamentous end of the capsules is usually defective the measurement of length includes only as far as the base of the filament. This length can be estimated with fair accuracy and serves as a convenient basis (100 per cent.) of proportions. It is understood that the present estimates are approximate, but they are probably not far from the mean of the species.

† This specimen could not be identified at the Jardin des Plantes. According to Duméril's description it is smaller than the specimens there preserved, measuring but 21 cm. in length (not counting terminal filament). It has also hook-like processes at the tips and sides of opercular valve. Locality unknown.

CLASSIFICATION OF CAPSULES.

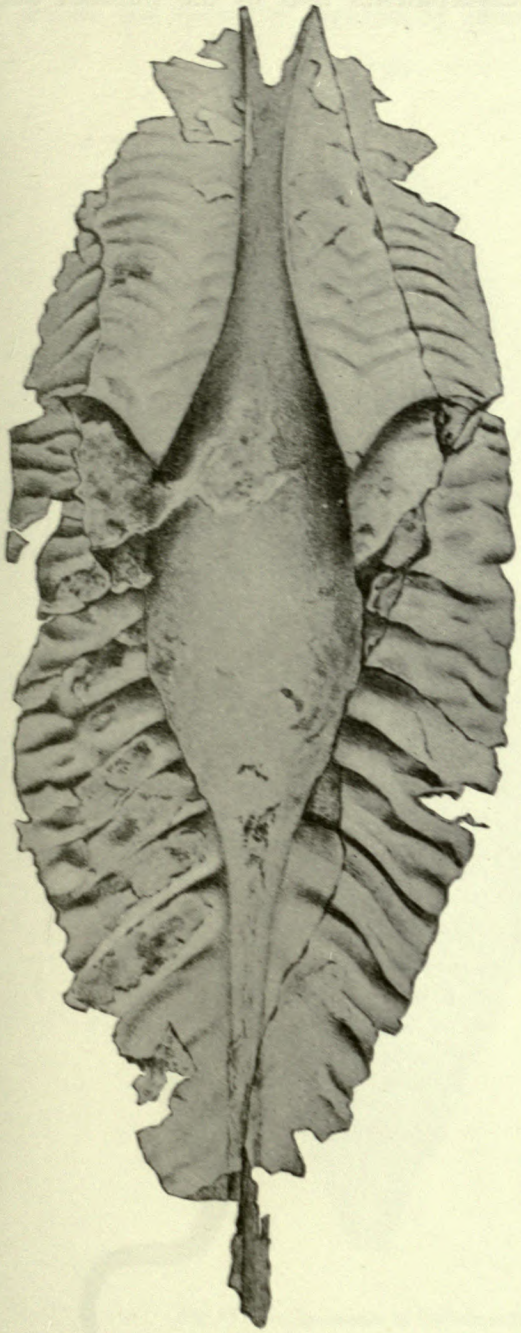


Fig. 14.—Egg-capsule of fossil Chimæroid, Ischyodus (Aletodus), from Dogger beds (Jurassic), Germany. After Jaekel. Actual size.

From the materials provided in the present table and figures the egg-capsules of Chimæroids may be classified on somewhat the following basis:

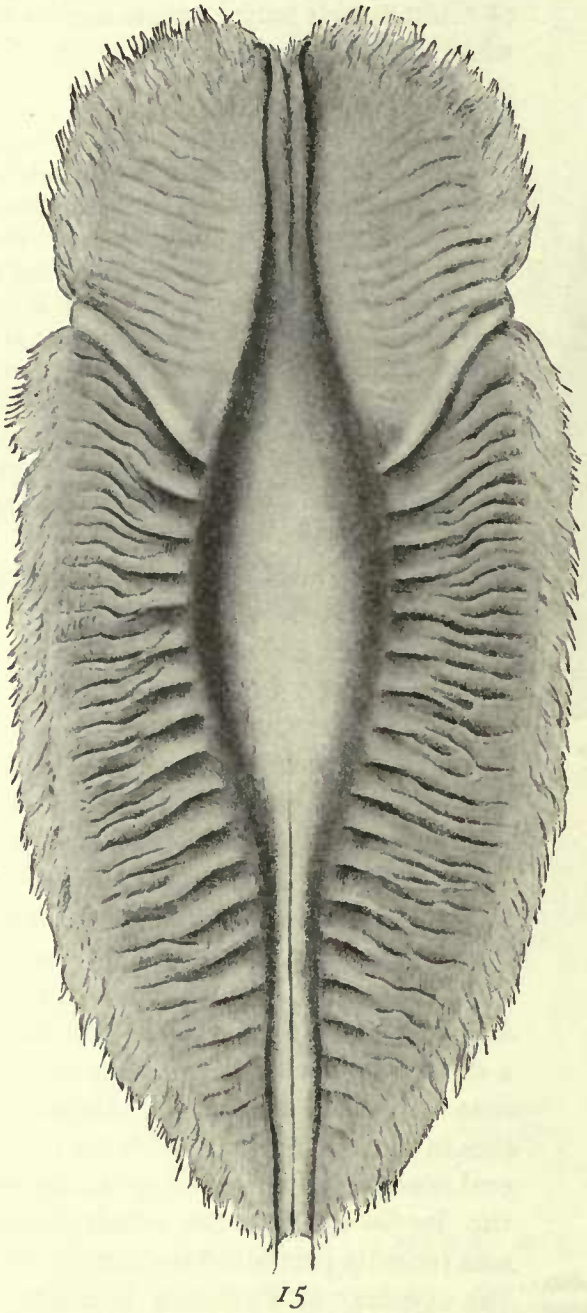
Callorhynchus. (Fig. 15 A–F.)

Capsules with case spindle-shaped; snout-sheath subequal in length to the tail-sheath; lateral web broad, exhibiting stout rugæ; of these a conspicuous pair proceeds outward from hinge of opercular valve. No serrulæ present, the opercular ridges merely separating to admit water, as in related structures in sharks. No caudal pores; in their place a slit on each side of tail-sheath opening on the ventral side in the angle between web and case. Anterior lip of operculum transverse, situated on dorsal side at a considerable distance from anterior margin of capsule. No dorsal keel. Heavy capsules, leathery and glabrous.

No capsules of Callorhynchus are known to be definitely associated with particular species, although many of the specimens preserved in museums are ascribed to "*C. antarcticus.*" From a study of the capsules of the species of Chimæra,* however, it is clear that the differences between the capsules described are such that we can not believe that they belonged to the same species. Thus the Chilean capsule (fig. 15), described by Jaekel as "*Cal. antarcticus*" (a synonym of *C. callorhynchus* of Valenciennes) is probably of a different species from the similar egg-case (fig. 15A) figured by Duméril, and this in turn is notably different from several specimens in the zoological museum of the Jardin des Plantes, which the writer was recently permitted to examine through the courtesy of Professor Vaillant. The latter capsules are accordingly figured

* Variation of the capsules within the range of the species was studied by the writer in the instance of *Chimæra colliei*. About eighty capsules were examined, but the variations were found different in character from those referred to in the present pages.

(fig. 15 B–F) from tracings of the specimens, and they will be seen to present a considerable range, both in proportional measurements and in the number and character of the rugæ and rugulæ.



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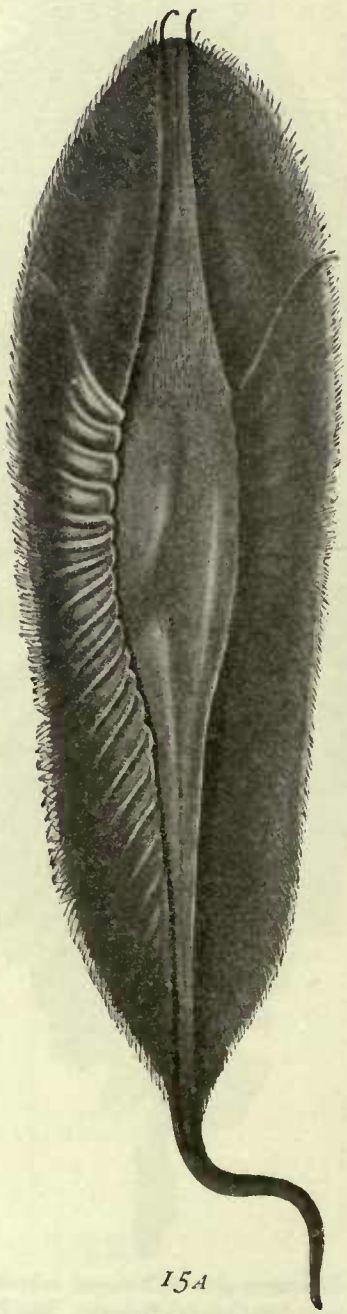


15A

Fig. 15.—Egg-capsule of Callorhynchus. From specimen collected in Chile by Plate. After Jaekel. Actual size.
Fig. 15A.—Egg-capsule of Callorhynchus. Locality unknown. After Duméril. About two-thirds actual size.

In further detail, the capsule, fig. 15 B (Cape of Good Hope), resembles most closely that of fig. 15 E (Magellan). It differs, on the other hand, in having the walls of the case more delicate and transparent, in spite of the fact that the Magellan speci-

men (or specimens) is much smaller in size. This difference, therefore, could hardly prove a matter merely of age. Another capsule (Chilean), fig. 15 D, is again quite unlike the specimen figured by Jaekel. It is almost a third larger in size, but nar-

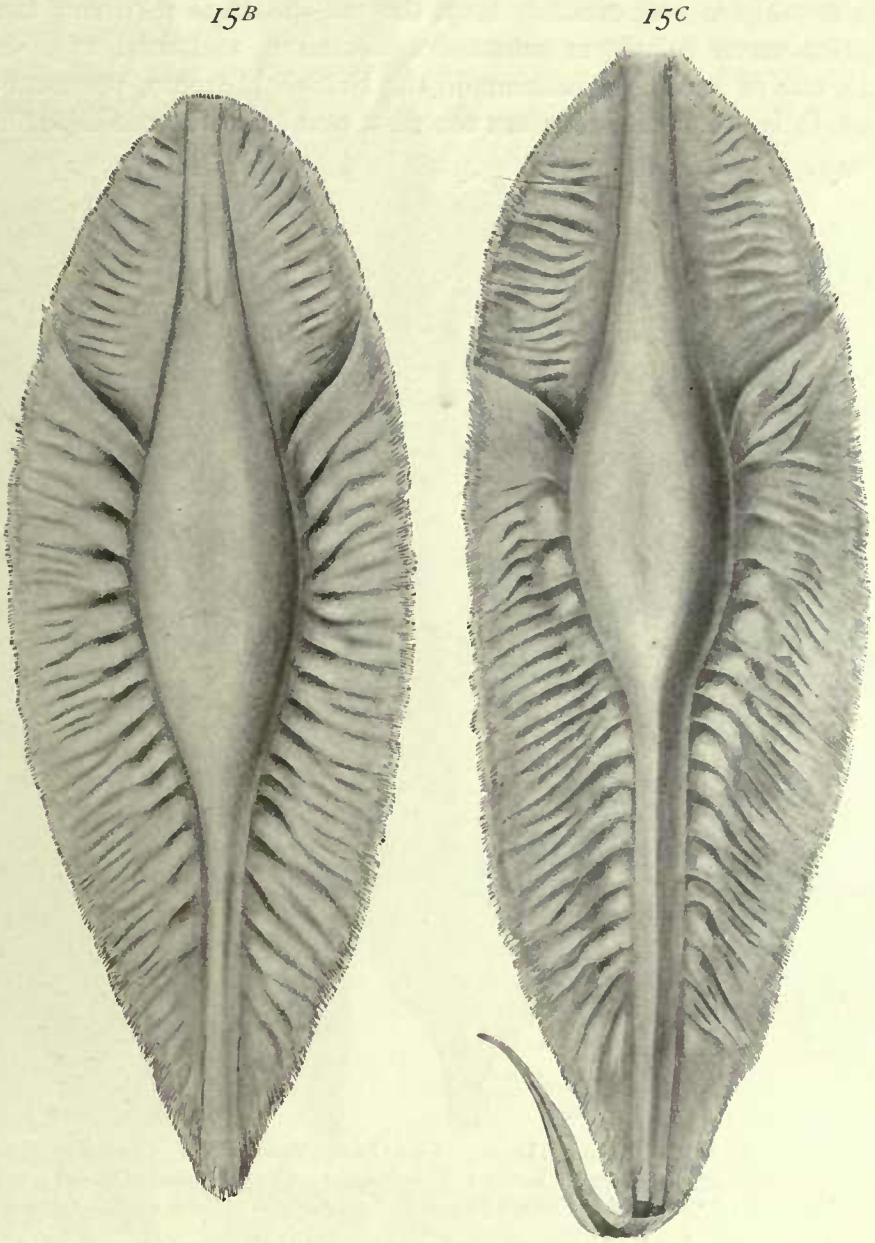


Fig. 15 B.—Egg-capsule of Callorhynchus. (Quoy and Gaimard.) From Cape of Good Hope. (Ventral aspect.) One-half actual size.
Fig. 15 C.—Egg-capsule of Callorhynchus. (Péron.) From Australia. (Ventral aspect.) One-half actual size.

rower proportionately. Its emphasized rugæ arising from the opercular hinge are more nearly transverse, and, unlike any other capsule of Callorhynchus known to the writer, it presents a thick, opaque case, margined by a thin, transparent web. In

the last regard it differs again from the capsule of fig. 15 E, in which the portion of the web in front of the opercular hinge is far more transparent than the posterior portion. Again, the capsule of fig. 15 C, although somewhat resembling that of fig. 15 B, differs notably in proportions; thus, the tail-sheath is relatively longer. The capsule is also much lighter in substance. A sixth and final capsule, fig. 15 F (Australian), one of several specimens in the British Museum, presents additional differences. It is much broader than the rest, and is notably deficient in rugulæ.*

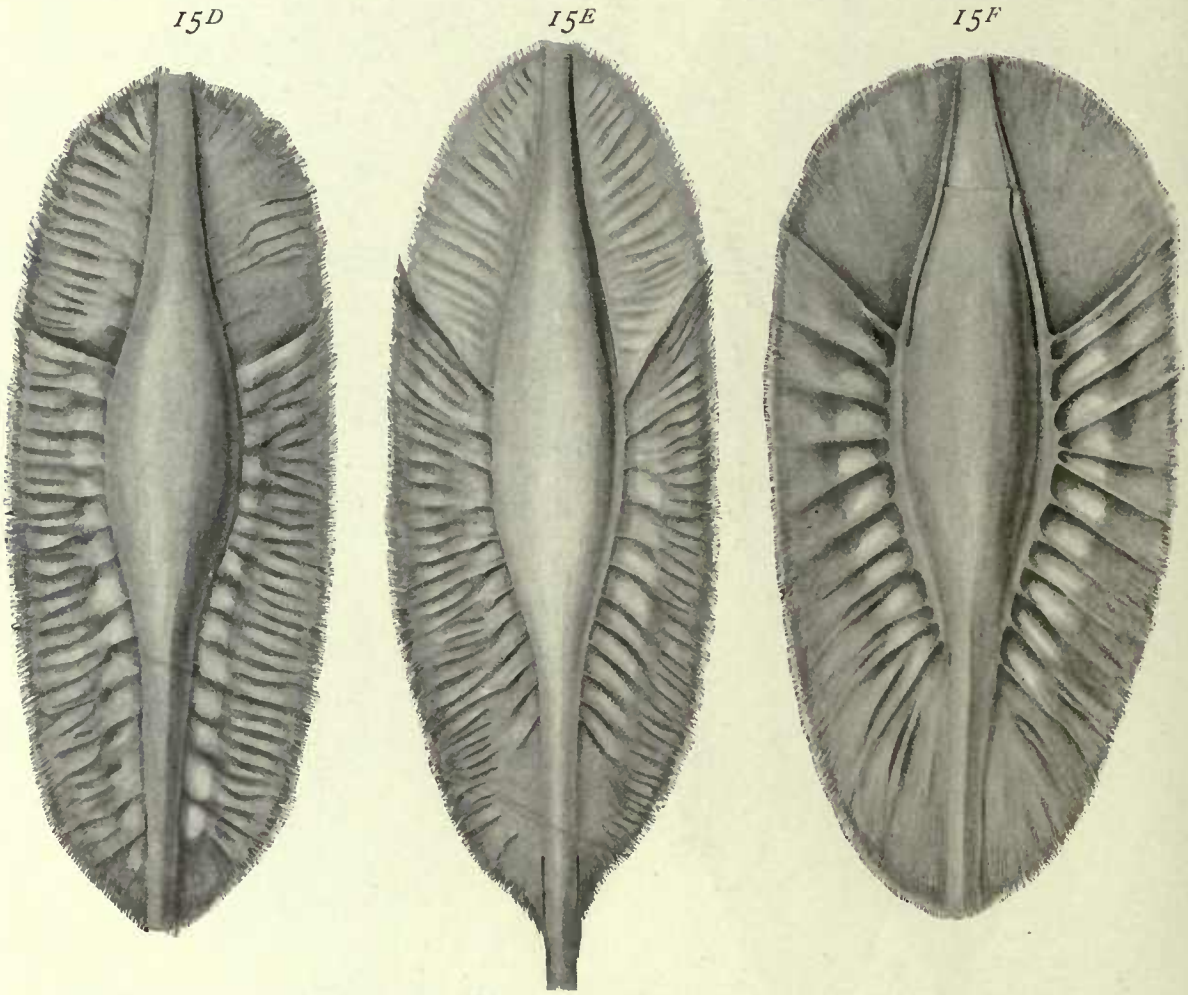
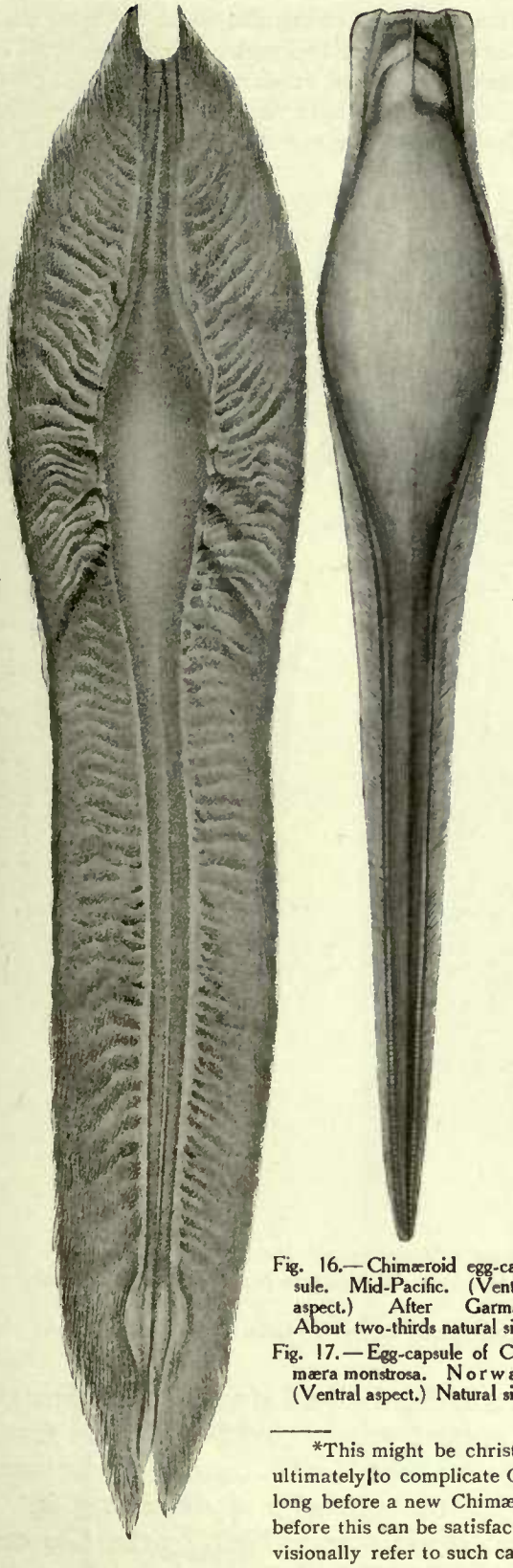


Fig. 15 D.—Egg-capsule of Callorhynchus. (Martinez.) From Chile. (Ventral aspect.) One-half actual size.
Fig. 15 E.—Egg-capsule of Callorhynchus. (Savatier.) From Magellan. (Ventral aspect.) One-half actual size.
Fig. 15 F.—Egg-capsule of Callorhynchus. (British Museum.) From Australia. (Dorsal aspect.) One-half actual size.

Specimens similar to the last mentioned appear in the museums of Copenhagen and of Harvard University.

Other Callorhynchid capsules include a fossil one, "Aletodus" (Ischyodus), and one of the curious elongated forms from the middle Pacific, which has recently been described by Garman. The first (fig. 13), lately discussed by Jaekel, proves so similar to the foregoing recent capsules that one may doubt the propriety of regarding it as having belonged to a separate genus. The second, Garman's cap-

*The specimens, four in number, in the British Museum, are essentially alike; two were collected near Dunedin, two near Hobart (mem. kindly furnished by Mr. Boulenger).



16 17

Fig. 16.—Chimæroid egg-capsule. Mid-Pacific. (Ventral aspect.) After Garman. About two-thirds natural size.

Fig. 17.—Egg-capsule of Chimæra monstrosa. Norway. (Ventral aspect.) Natural size.

sule (fig. 16), differs widely from other recent forms. It has thus a remarkably long tail-sheath; is provided with a distinct type of lateral web, for its rugæ are few in number and restricted to the region of the trunk-case, and there are no conspicuous rugæ arising from the hinge of the opercular flap, dividing a precardinal from a postcardinal lateral web, as in the other forms.

These differences are so striking that I am quite convinced that this capsule represents a new genus.* Garman himself tells us nothing of its antecedents, and as he on one page refers to it as belonging to *Callorhynchus antarcticus* and on another to *Callorhynchus callorhynchus*, I infer that he attributes it to the latter species and that he regards these terms as synonymous.

Chimæra.

Capsules somewhat tadpole-shaped, with large trunk-sheath, short snout-, and long, tapering tail-sheath; lateral web narrow, with rugæ faint, if present at all. Opercular flap extends forward to end of case; serrulæ present, beginning far forward, a part of the complicated apparatus of opercular ridges (*cf.* pl. III, fig. 17, A, B, C); caudal pores many, opening on both dorsal and ventral sides. A dorsal keel present. Capsules thin, parchment-like, smooth or slightly ridged. The species differ in well-marked details, *e.g.*, in width of lateral web, length of tail-sheath, modeling of trunk- and snout-case, texture, number of serrulæ, etc. If arranged in a comparative series (*cf.* table, p. 30, and figs. 17, 18, 21, 22), *C. colliei* stands closest to the type of Garman's capsule, and *C. mitsukurii* is obviously the most specialized.

*This might be christened and specified by a systematist who does not hesitate ultimately to complicate Chimæroid literature in the matter of synonyms. It may be long before a new Chimæroid is fished from the mid-Pacific and it may be a century before this can be satisfactorily fitted to "Garman's capsule." Let us therefore provisionally refer to such capsules according to the names associated with them—thus under Callorhynchids we may refer to the "Martinez capsule," "Péron capsule," etc.

Harriotta(?).

Capsule (fig. 19) with case outlined like a short-handled spoon; lateral web wide and evenly transparent, strengthened by an even series of thickened costal ridges. Dorsal valve terminates in a broad transverse lip subterminal; its lateral rims have ruffle-like serrulæ, which are most marked midway between hinge and anterior lip, and fade away anteriorly and posteriorly. No dorsal keel; on the contrary, a shallow groove extends along the dorsal wall of caudal sheath. Caudal pores in a series of decided slits; the largest, in the middle of the series, open ventrad, although they appear also on the dorsal side as a marked surface feature of the capsule. Capsule smooth, parchment-like, pale.

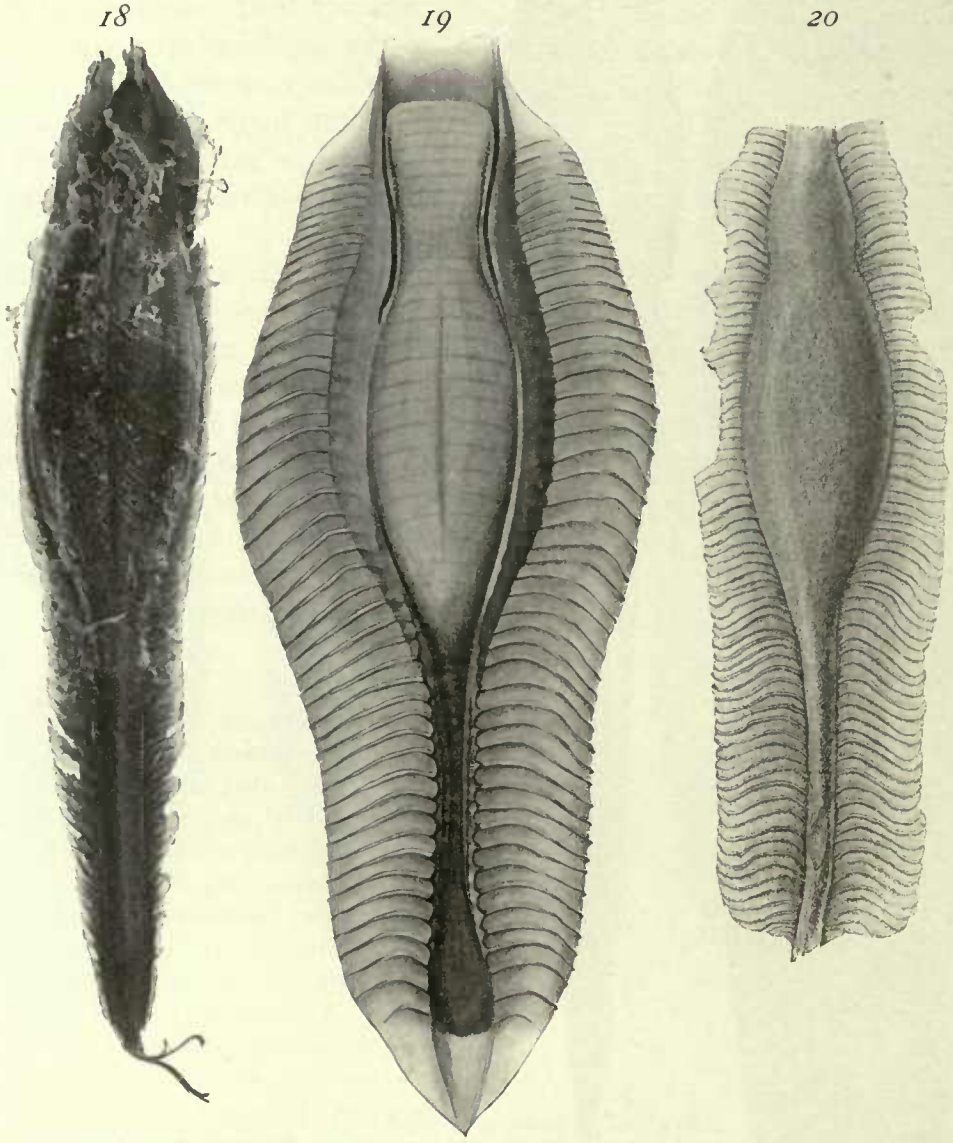


Fig. 18.—Egg-capsule of Chimæra colliei. Puget Sound. (Ventral aspect.) Natural size.
Fig. 19.— Egg-capsule of Harriotta (?). North Atlantic. After specimen preserved in U. S. National Museum. (Ventral aspect.) Natural size.
Fig. 20.— Egg-capsule of Rhinochimæra indica ("Callorhynchus indicus"). Indian Ocean. After Alcock. (Ventral aspect.) Three-quarters natural size.

This interesting specimen is preserved in the National Museum at Washington, where it bears the number 22793. The present writer is indebted to the Curator of the Department of Fishes, Mr. Barton A. Bean, for his courtesy in bringing it to his attention, and to the Museum for the privilege of describing it. Its history is briefly as follows: It was taken, 1879 (on trawl line), by the Gloucester fishing vessel of Capt. G. A. Johnson, in water of 375 fathoms, lat. 42° 47′, long. 63° 10′. It obviously does not belong to the foregoing genera, but from its resem-

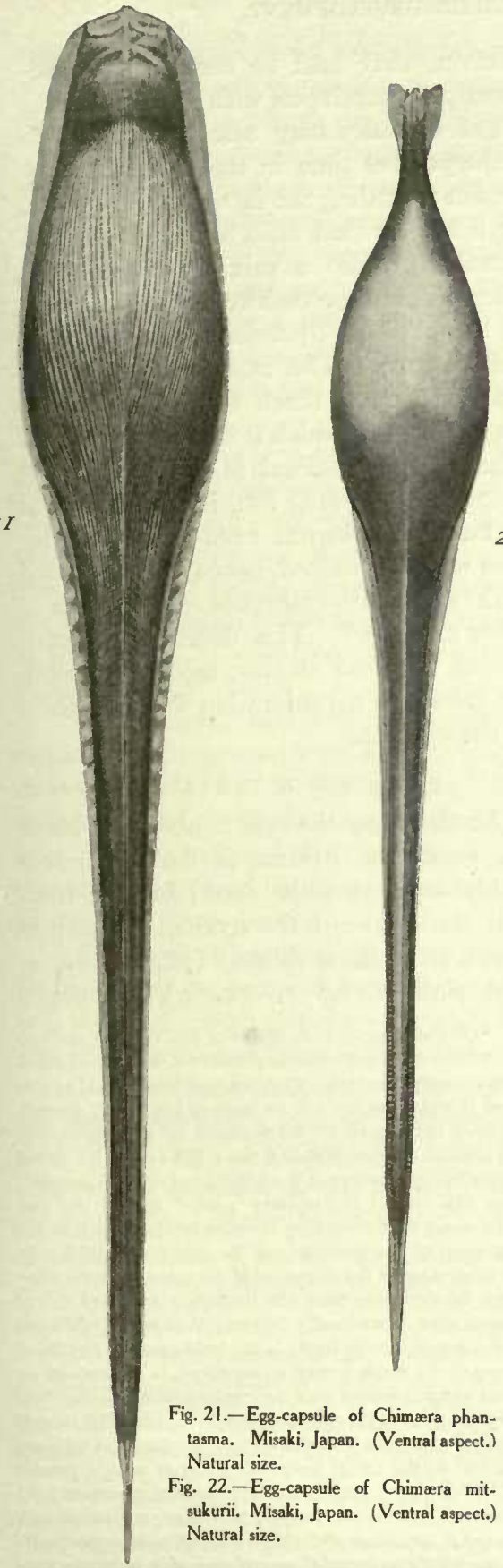


Fig. 21.—Egg-capsule of Chimæra phantasma. Misaki, Japan. (Ventral aspect.) Natural size.

Fig. 22.—Egg-capsule of Chimæra mitsukurii. Misaki, Japan. (Ventral aspect.) Natural size.

blance to Rhinochimæra it evidently belonged to a similar fish. It is thus to be attributed, with strong probability, to the only Chimæroid of this character known from the region in which it was taken, *i. e.*, Harriotta.*

A second capsule (fig. 20), hitherto associated with Callorhynchus, should provisionally be placed with the present genus. Although collected in the Indian ocean, it resembles closely the capsule from the Atlantic, having the same type of lateral web, costæ, and subterminal opercular margin.†

Rhinochimæra.

Capsule with case spindle-shaped; snout-sheath stouter and thicker than tail-sheath; lateral web wide, its outer margin transparent, strengthened by a regular series of tapering costæ. Lip of dorsal valve ends in a narrow, delicate lip, subterminal. Serrulæ low and faint. No dorsal keel; in its place a shallow groove extends along the dorsal wall of the caudal sheath. Caudal pores similar to those in Harriotta (?). Capsules smooth, dark-colored, hornlike.

The capsule shown in fig. 23 has been definitely associated with the species *R. pacifica*. It differs notably from the Indian capsule in proportions, in the number and character of its costæ, and in its operculum.

On the foregoing pages the egg-capsules of Chimæroids have been referred to in considerable detail, since by a comparison of their characters light is thrown upon the problem of Chimæroid descent. For it is clear that the different species of Chimæroids produce capsules specifically distinct; and it follows, therefore, in the light of evolutional analogies, that the fishes which produced the more differentiated capsules are the descendants of those in which simpler capsular structures prevailed. It follows, also, conversely, that the forms which have the simpler capsules are apt, in this and other regards, to represent more closely the common ancestor. This evidence,

**Harriotta* has been taken between lat. 36° and 40°, long. 70° and 75°; from greater depth, however—700 to 1,100 fathoms. The latter difference is not all-important, as by many analogies spawning might well occur at a lesser depth.

†The writer recently examined this specimen in the Calcutta museum, through the courtesy of Major Alcock.

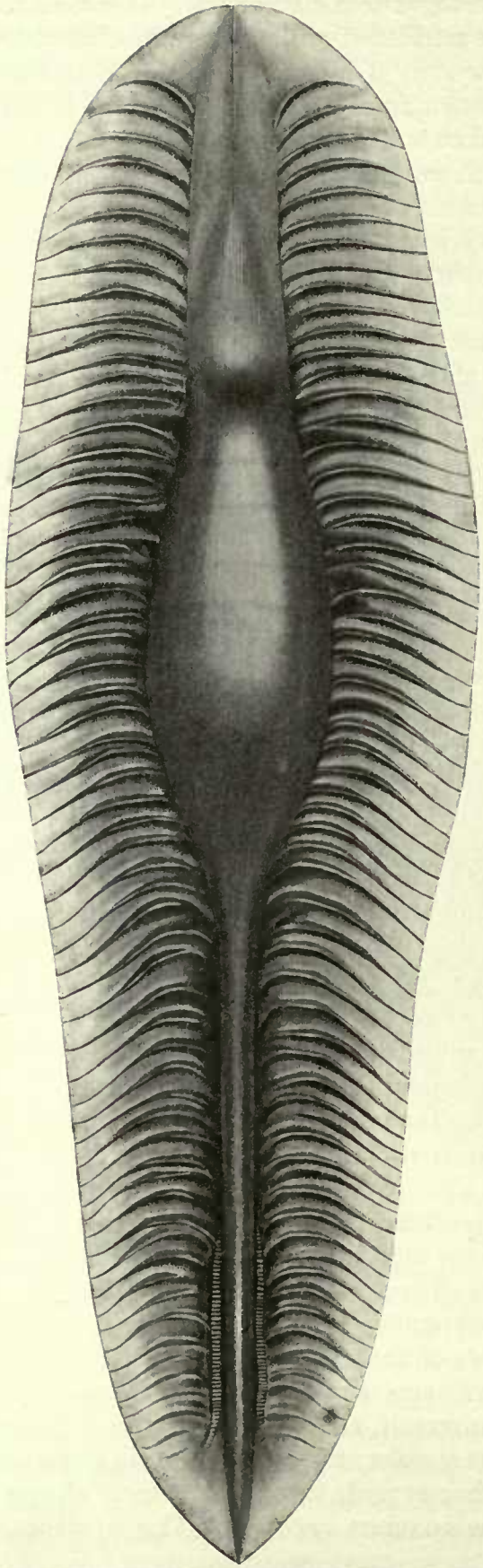


Fig. 23.—Egg-capsule of Rhinochimæra pacifica. Misaki. (Ventral aspect.) Natural size.

however, may best be considered subsequently in correlation with similar facts.

The capsules may also be referred to at the present time in the evidence they present regarding the factors of evolution; for it is clear that such highly specialized capsules provide a valuable check upon the evolutional process from the standpoint of the obvious "prevision" which they demonstrate. The capsule is, in short, adapted not so much to the egg as to the young fish which it will later contain. Thus it is specialized in accord with the shape of the young fish, its position, and its late physiological needs, all to a degree which is, indeed, probably unequaled in the secondary embryonic membranes of other animals.* This degree of specialization becomes clearer, moreover, when we take into consideration the formation of the capsule.

FORMATION OF THE CAPSULE.

At the time the egg is about to leave the ovary the oviduct is flaccid and is richly suffused with blood; in fact, from this time onward the oviducal sinus† in which they lie is dilated (plate I, fig. 4, and plate II, fig. 5, *ovd. s.*), forming a

Cf. Dean, 1904, Biol. Bulletin, vol. VII, pp. 105-112.

† These sinuses arise in the mesovaria, the walls of which do not become apposed. They are thus longitudinal sacs of blood in which the oviducts lie more or less freely, depending upon the degree of development of the egg-capsule (*cf.* plate II, fig. 5, and plate I, fig. 4, left oviduct). In the former figure, however, this condition is not seen favorably, since the oviduct is purposely pushed against the wall of its sinus, thus dislodging the opaque blood, so that the structures of the oviduct can be better described. In the latest stage in the formation of the capsule, on the other hand, the sinus is so filled with the enlarged oviduct that in ventral view it can hardly be seen; thus in the figure the oviducts appear to lie freely in the body-cavity. The blood supply in the sinus, it may be remarked, is maintained by direct communication with the cardinal (not to complicate the problem as to the relations with the renal portal) blood-cavities. Between the lines where the mesovarial folds are attached to the dorsal body wall a row of ostia is present (pl. I, fig. 4, *o*). This method of increasing enormously the oviducts' blood (venous) supply is evidently correlated with the rapid formation of the highly complicated egg-capsule. It can hardly be regarded as evidence of a primitive gonadial sinus, and we are led to conclude that morphologically the veins of the mesovarium have coalesced, leaving ostia as vestiges of the gonadial veins, *e. g.*, of sharks.

remarkable venous outlet, and the arterial supply is also highly developed, branches of the oviducal artery passing backward along the oviduct and dividing into an elaborate series of transverse branchlets.*

The oviduct itself undergoes striking changes to accomplish step by step the stages in the formation of the capsule. To follow these briefly, the oviduct contracts cephalad when the egg is received, and holds it in the cavity dilated in the posterior region of the capsular gland. Here it is that the walls of the oviduct form folds and ridges and by these are able to model the secretion of the gland into the beginnings of the capsule. From such a position the early capsule was obtained which is figured in plate III, figure 12. Its shell was papery, whitish (with but a trace of color), and so frail that it could not be removed unbroken with the contained egg.

The exact mode of folding of the walls of the oviduct to produce the details of the capsule need not be given in detail. The growth in the capsule continues, as shown in plate III, figs. 13, 14, 15, and 16, the tail-sheath and its appendage of the case being the last portions formed. The fact that the anterior part of the case is finished before the tail-sheath was often taken advantage of by the writer in his effort to secure embryological material, for he found that such an egg as shown in plate II, fig. 8, could be safely incubated for earlier stages if the base of the tail-sheath was kept closed, *e. g.*, by a ligature.

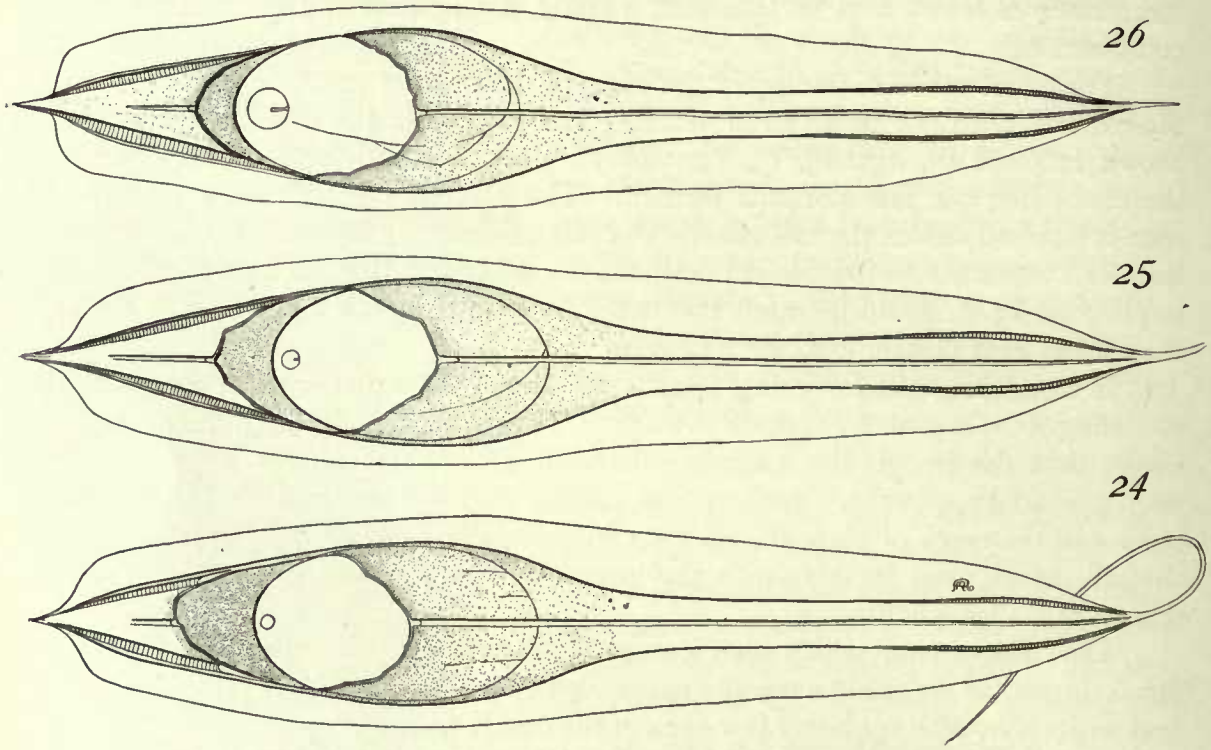
In comparing the foregoing figures one observes a number of details as to the modeling of the capsule from stage to stage. The earliest condition (plate III, fig. 12), shows that the tip of the capsule, although delicate, is almost complete, with opercular folds, serrulæ, apex, lateral ridges, and the beginnings of the dorsal keel. In the stage of plate III, fig. 16, the capsule is practically complete, save for the tail-sheath, and in this stage the lateral webs are widest, suggesting the conditions of Callorhynchus.

The oviduct from which such a stage is taken as that shown opened in plate II, fig. 6, forms, as we could naturally expect, an exact mold for the capsule. Thus we find a cervix, *c*, with sphincter (for apex of the case); distinct creases, *l. w.* (for lateral webs); a thickened tract, with folded margins and with median groove, *d. k.* (for dorsal wall of case, opercular folds, and dorsal keel). As the tail-sheath was not yet developed in this capsule, the corresponding region of the oviduct, *t. s.*, is still contracted; but at the sides we note the broader folds, *r*, in which the rugæ are laid down; also at *t. o.* the deep recesses below the capsular gland in which the terminal organ comes to be formed. At a subsequent stage the lateral webs are strengthened by a process of folding, which causes them to become narrower (*cf.* plate II, fig. 10, and plate III, fig. 16); and at the same time the tail-sheath is laid down (plate I, fig. 1).

In the latter process the sheath itself, with the beginnings of its caudal pores, is formed before the adjacent web (plate II, fig. 7), and when this is completed there remains to be formed only the capsular filament and adhesive organ. By this time, however, the capsule has acquired such a phenomenal length that it extends from the oviducal (*i. e.* retroanal) opening forward to the anterior wall of the body-cavity

* The oviducal artery divides into four branches when it reaches the anterior end of the capsular gland, two becoming dorsal, two ventral, and thus they proceed, bilaterally arranged, as far as the posterior portion of the oviduct (*cf.* plate I, fig. 1; plate II, figs. 5 and 7).

terminating near the cardiac region. To add, therefore, a couple of inches to the length of the capsule involves a serious problem in the matter of space. This has been solved as follows : The capsule is gradually released, so that it comes to project from the fish's body ; at first the apex appears at the mouth of the oviduct, then the trunk-sheath, then the tail-sheath (fig. 12). If at this time the egg is dislodged, an abortive terminal results, as in plate II, fig. 10. If it remains, the process in the formation of the capsular filament and terminal organ progresses as seen in plate I, fig. 4. The capsule now protrudes as far as the base of the filament, and with this



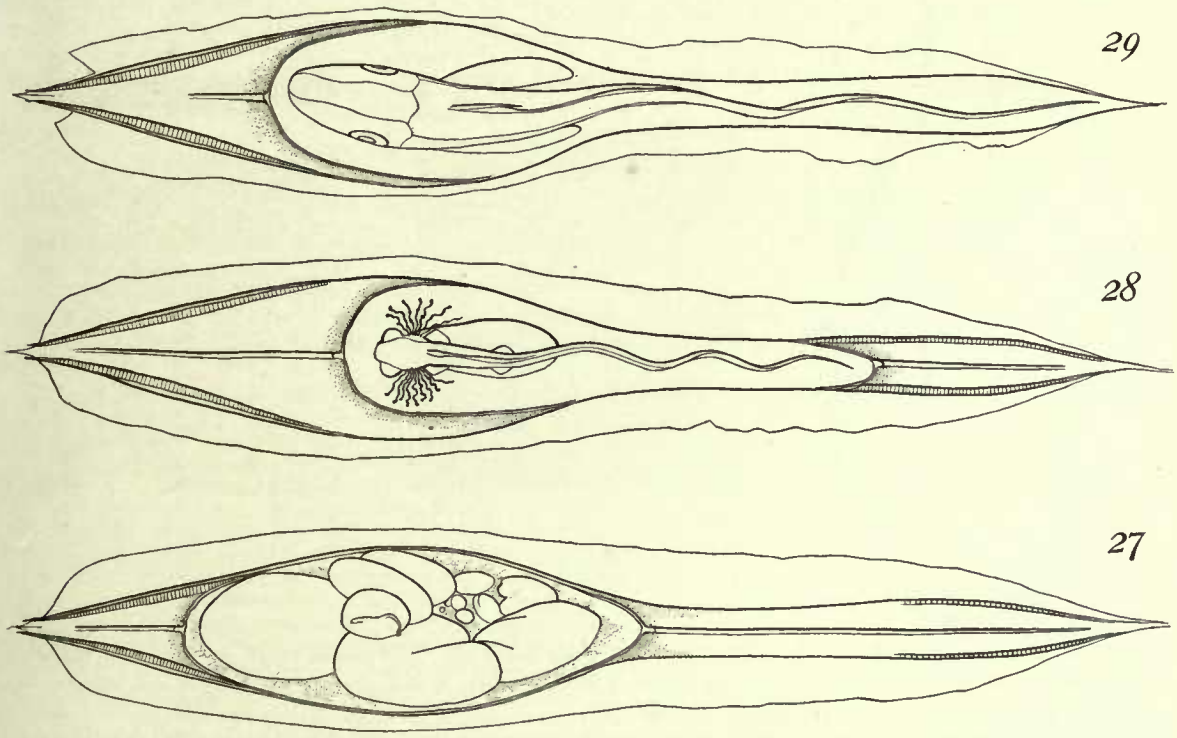
Figs. 24-26.—Egg-capsules of Chimæra colliei, partly opened, so as to show egg and young. Natural size.
24. Late blastula (about 9 days). 25. Early gastrula (about 19 days). 26. Late gastrula (about 24 days).

protrusion occur many changes in the oviduct (*cf.* plate II, fig 4, and plate II, fig. 6), *e. g.*, its diameter becomes greatly constricted and its dorsoventral characters and web creases obsolescent ; it also loses its earlier differentiation into trunk-sheath and tail-sheath forming portions, and its vaginal region is extended headward, the remaining part of the oviduct becoming correspondingly reduced. All these changes are to the obvious end of molding the long capsular filament and the bulbous terminal organ (plate I, fig. 4, *c. f.*, and *c. o.*). For the formation of the latter serves a special region of the capsular gland, *i. e.*, its hindmost zone, a portion pinkish in color, provided with the recesses into which the terminal organ has been traced.*

* Finally, a note may be given as to the probable mode of attachment of the capsule (*cf.* pp. 26, 27.) It is evident that the oviduct can be greatly evaginated at the time the egg is deposited (plate I, fig. 2), and with this phenomenon is evidently connected the forward extension of the cervix (*cf.* plate I, fig. 4, and plate II, fig. 6). We may thus conclude that at the cervix, then, the bulbous organ of attachment can be held by the fish even when the oviducts have been greatly everted ; and it would naturally be by such elongated, even finger-like, processes that the fish could press the filamentous ends of the capsules against the object of attachment, *e. g.*, a rock fragment, and thus secure their adhesion.

Before describing the various stages of Chimæra (*C. colliei*) a brief survey of the general plan of development might be given (*cf.* Biol. Bulletin, 1903, vol. IV, No. 5, pp. 270–286):

The development is shark-like (figs. 24–29). In early stages a small germinal area is present. In this polyspermy occurs, then a cleavage, in which, however, surface furrows are retarded. The early gastrula suggests somewhat closely the condition in shark, or rather in ray, but the blastopore appears *near* instead of *at* the margin of the blastoderm. The embryo develops a long, delicate tail, external gills, and a head terminating in a conspicuous frontal "lobe." It absorbs the yolk-



Figs. 27-29.—Egg-capsules of Chimæra colliei, partly opened, so as to show egg and young. Natural size.

27. Early embryo (about 32 days), showing subdivision of yolk material.
28. Late embryo (about 5 months), showing external gills and miniature sac. At this time the embryo is bathed in a heavy milky fluid resulting from continued subdivision of yolk masses.
29. Young Chimæra at about the time of hatching (? eight months). The capsule at this period is greatly weathered and develops a tension which probably aids the operculum in springing open and permitting the young to escape.

sac, and before hatching becomes large in size and has many features of the adult, *e. g.*, mixipterygia in the case of the male. By far the most remarkable feature during this process of development is the behavior of the yolk. This undergoes vacuolization, followed by fragmentation. Of the yolk a small portion only is inclosed within the sac of the young; the remainder continues to fragment, forming a creamy mass which nourishes the embryo *via* external gills and gut. The fragmentation, we have reason to believe, is an extreme modification of the process of cleavage.

THE EGG AND ITS MEMBRANES.

In the newly deposited capsule the egg measures 35 by 20 by 12 mm., but it is smaller, together with the capsule, if taken from young fish (*cf.* the size of the capsules shown in plate II, fig. 10, and plate III, fig. 17), as is also the case in selachians (Rückert). Its consistency becomes less fluid-like as development advances; thus, shortly before breaking from the ovarian membrane, the egg has so little consistency that it will flatten out to the diameter of about 45 mm. (plate II, fig. 5). Its ellipsoidal outline is assumed when inclosed in the capsule. It will, however,

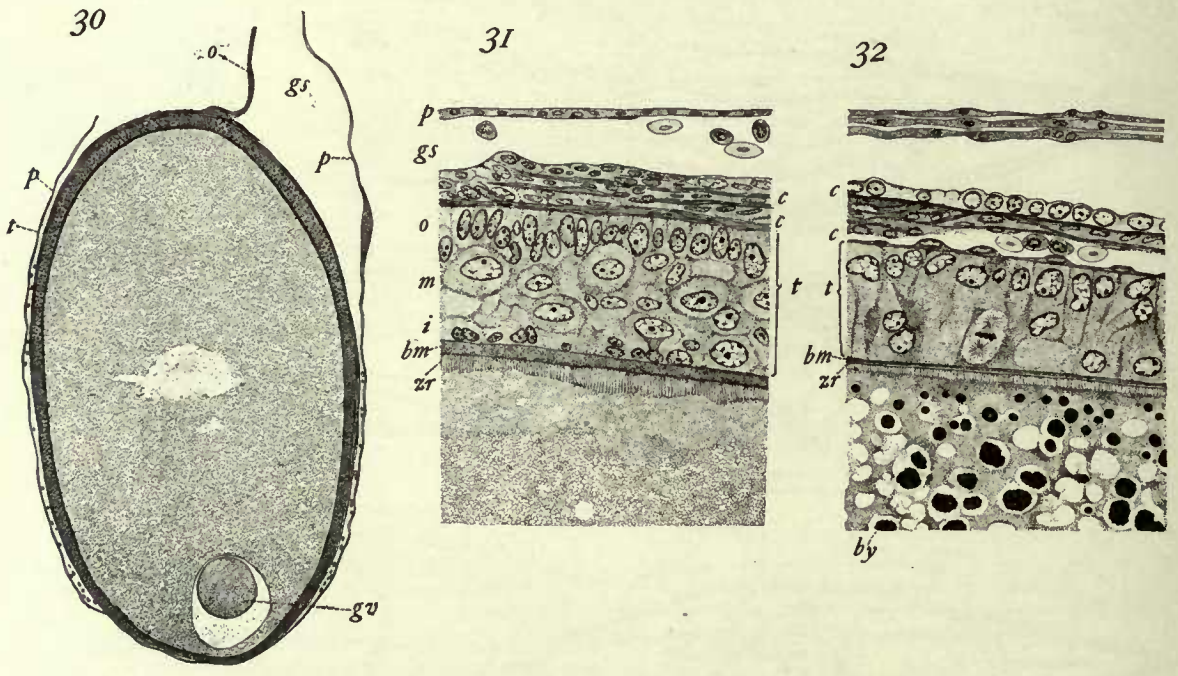


Fig. 30.—Early ovarian egg of Chimæra colliei. Section through major axis of egg. *gs*, Gonadial sinus; *gv*, germinative vesicle—around it the extent of the space indicates the size of vesicle before fixation; *o*, stalk attaching egg to ovary and inclosing the arterial blood supply; *p*, peritoneum; *t*, tunic (= granulosa).

Figs. 31 and 32.—Sections of the marginal region of ovarian eggs (the first measuring about 5 mm. in diameter, the second about 15 mm.), indicating changes in the tunic and the development of yolk. *bm*, Basement membrane (between the tunic and the egg); *by*, botryoidal yolk masses developed in vacuoles in germinal yolk; *c*, layers of connective and vascular tissue theca in ovarian membrane surrounding egg; *gs*, gonadial sinus; *p*, peritoneum; *t*, tunic of ovarian tissue inclosing egg (follicular epithelium); *i*, inmost layer; *m*, middle layer; *o*, outmost layer; *zr*, zona radiata. × 585.

present an almost spherical form (horizontal outline 25 by 20 mm.) if the constricting capsule be opened (plate II, fig. 8). In later stages it has the consistency of thick cream.

THE OVARIAN MEMBRANES.

Comparison with corresponding stages in shark (Pristiurus) shows that the wrappings of the ovarian eggs of Chimæra are the more complex. In early stages of the latter the ovarian tunic is thicker and its nuclear elements more abundant and more evidently specialized. Thus in fig. 30, which shows in section an egg of about 5 mm., one notes the thickness of the tunic; this (greatly enlarged) is shown in

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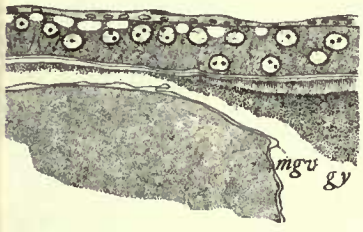

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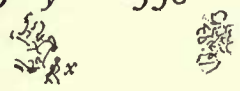

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is clearly connected with a nucleus of the middle layer. In some cases such a relationship is demonstrated by dividing nuclei, which, it may be remarked, exhibit sometimes direct, sometimes indirect division. At the surface of the egg is a sharply marked membrana limitans; below this, irregular in thickness, a zona radiata, probably homologous with the well-known layer in eggs of other fishes. Below this the egg shows an outer finer layer and an inner coarser or reticular layer, in which large vacuoles frequently occur. At a somewhat later stage (egg measuring about

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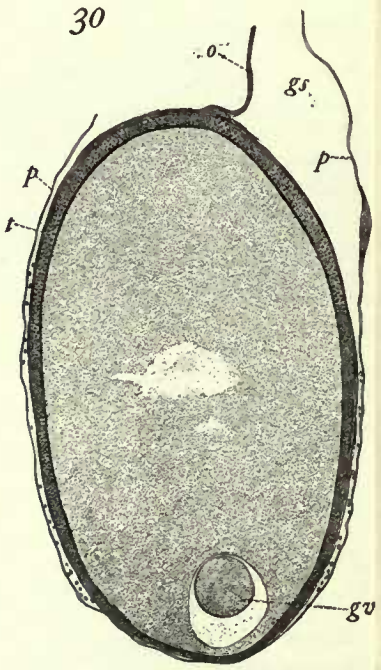

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THE OVARIAN MEMBRANES.

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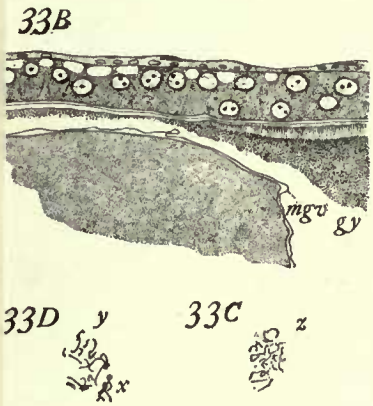

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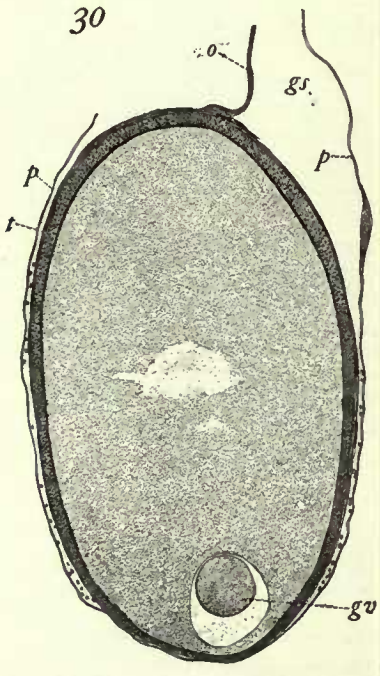

Fig. 30.—Early ovarian egg of Chimæra col
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THE OVARIAN MEMBRANES.

Comparison with corresponding stages in shark (Pristiurus) shows that the wrappings of the ovarian eggs of Chimæra are the more complex. In early stages of the latter the ovarian tunic is thicker and its nuclear elements more abundant and more evidently specialized. Thus in fig. 30, which shows in section an egg of about 5 mm., one notes the thickness of the tunic; this (greatly enlarged) is shown in

fig 31; here it will be seen that the tunic, although syncytial in character, is clearly divided according to its nuclei into three layers—outmost, middle, and inmost. In the outmost layer the nuclei are small and closely compressed—oblong, therefore, in form—and directed ecto-entad; in the middle layer they are large and diffuse; in the inmost, small, irregular, and closely apposed to the basement membrane. Between the outmost layer of the tunic, *o*, and the gonadial sinus, *gs*, the tissue of the ovary contains numerous strands of connective tissue interspersed with plasma spaces, *c*; it is from these, doubtless, that nutriment is passed through the specialized tunic to the inclosed egg. During this process it may be assumed that the various types of nuclei of the tunic play definite parts; thus the closely compacted nuclei of the outmost layer purvey nutriment from the plasma spaces (and capillaries) to the dilated elements of the middle layer. These again transfer their nutriment to the small nuclei which are closely apposed to the egg.

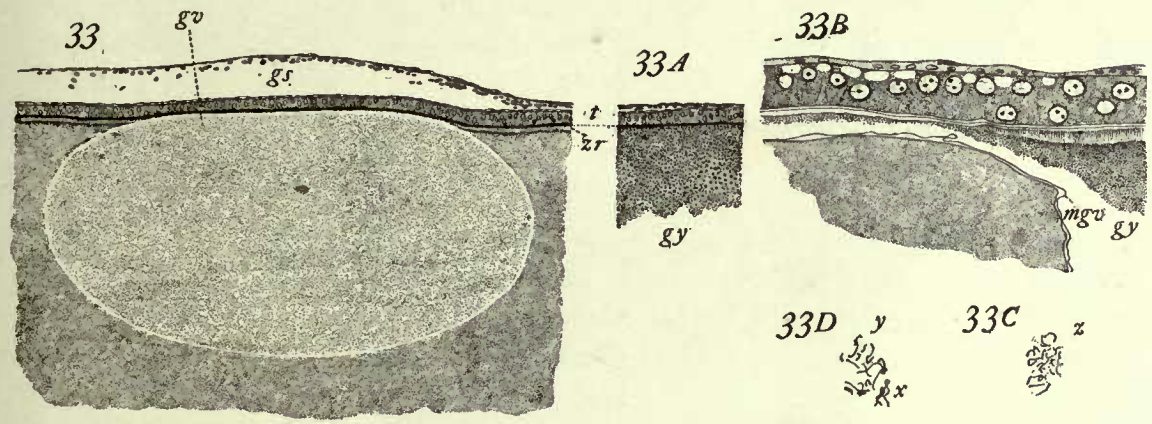


Fig. 33.—Section of region of germinative vesicle of well-grown ovarian egg (about 20 mm. in diameter). *gy*, Germinal yolk; *gs*, gonadial sinus; *gv*, large germinal vesicle containing near its center a group of chromosomes; *mgv*, limiting membrane of germinal vesicle; *t*, tunic; *zr*, zona radiata.

Fig. 33A.—Detail of preceding section from point at side of egg, showing absence in this region of the zona radiata. In this region yolk granules are developed in numerous minute vacuoles.

Fig. 33B.—Detail of section of fig. 33, taken at a point where the side of the germinal vesicle recedes from surface of egg. *gy*, Germinative yolk; *mgv*, membrane forming wall of germinal vesicle; *t*, tunic, showing large vacuoles; *z*, zona radiata. This will be seen to extend only over the margin of the vesicle. Between the vesicle and the adjacent tunic there extends only a thin peripheral layer of germinative yolk.

Figs. 33C and 33D.—Detail of chromosomes shown in fig. 33 (two sections). × 385.

The differences in the nuclei of the tunics are apparently physiological, since intergrading forms occur; thus in the figure cited a nucleus of the inmost layer is clearly connected with a nucleus of the middle layer. In some cases such a relationship is demonstrated by dividing nuclei, which, it may be remarked, exhibit sometimes direct, sometimes indirect division. At the surface of the egg is a sharply marked membrana limitans; below this, irregular in thickness, a zona radiata, probably homologous with the well-known layer in eggs of other fishes. Below this the egg shows an outer finer layer and an inner coarser or reticular layer, in which large vacuoles frequently occur. At a somewhat later stage (egg measuring about

15 mm.) the conditions of the tunic have changed. It has become thinner (fig. 32) and has modified its structures considerably. In place of the differentiated inmost, middle, and outmost layers, an outer layer is alone conspicuous and even here the nuclei have not the crowded character of the earlier stage ; the inmost and middle layers have merged, forming a somewhat indefinite layer, poor in nuclei. In some cases markings in the (partial) syncytium indicate that the tunic is in places but one cell thick. Indirect divisions sometimes occur. The entire structure of the tunic suggests that closer physiological relations exist between the vascular supply, on the one hand—plasma spaces, as in *c*, having now extensively drawn together into

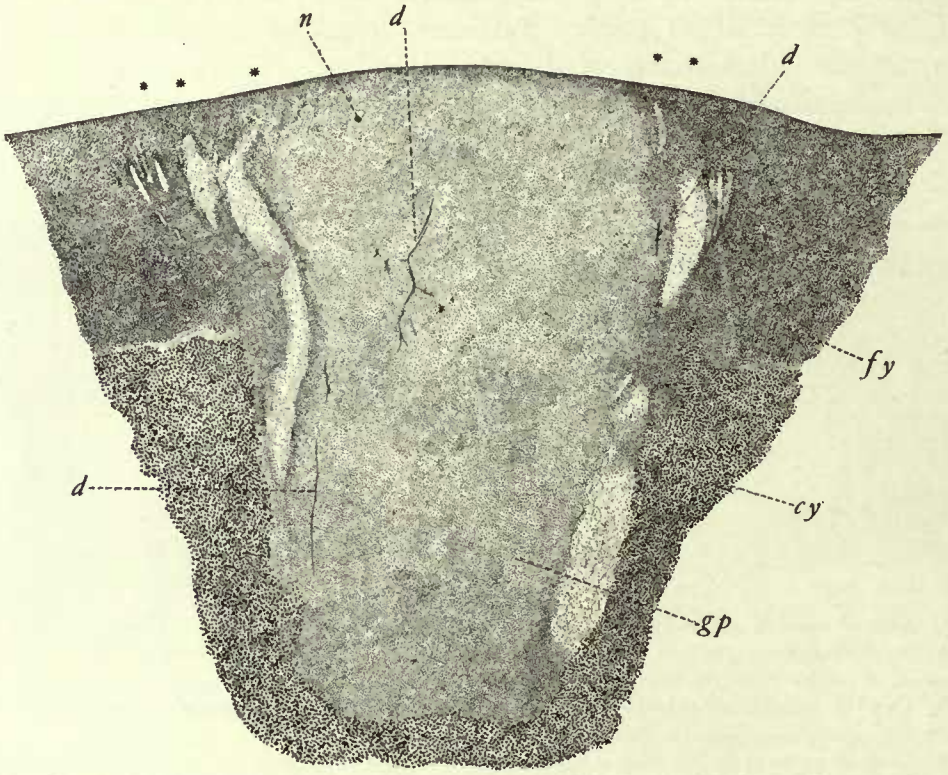


Fig. 34.—Section of germinal region of egg of Chimæra colliei during stage of early fertilization. *cy*, Coarse yolk; *d*, dendritic lines marking paths of sperms; *fy*, fine yolk; *gp*, germinal area extending as a plug-shaped mass deep into the egg; *n*, nuclei, sperm, and egg fusing. Under the points marked with asterisks (*) vacuoles occur which separate masses of fine germinal yolk and are usually found to contain sperm nuclei.

capillaries—and the egg on the other. This physiological process is doubtless aided by the thinning of the membrana limitans, *bm*, and of the zona radiata. And as an indication that the nutriment is being passed rapidly into the yolk we observe that even close to the surface of the egg large yolk masses are appearing.

In a final stage of the ovarian egg the tunic is still further diminished in thickness (figs. 33, 33 A). It is reduced, in fact, to a single-celled layer, of which the nuclei are usually disposed nearer the outer wall in the same niveau. Sometimes, however, they are closely apposed to the inner wall, but in all cases they are of the same general character (fig. 33 B), *i. e.*, spherical nuclei, with sharply marked membrane, showing but faint traces of chromatin meshwork, but with one or two con-

spicuous nucleoles. Cell boundaries are sometimes better seen than in earlier stages, and large vacuoles are present near the tunic's outer wall; surrounding this the ovarian stroma is reduced to practically a single-celled layer, which now alone separates the tunic from the blood in the large gonadial sinus (fig. 33, *gs*). Comparison with earlier stages thus indicates—paradoxical as the statement reads—that the arterial supply of the developing egg is progressively diminished and the venous supply progressively increased.*

The foregoing details are given, since they indicate the complexness of the problem of the growth of the egg in Chimæra. There here exist at various stages not a tunic of an almost unvarying character, as apparently is the case in sharks, but one which in earlier stages is shark-like, but which later changes progressively, diminishing its thickness and reducing the number of its component elements, to the end that each cell of this membrane comes in immediate contact on the one hand with the egg and on the other with the nutritive fluid. It is further clear that the elements of the tunic acquire changed physiological characters as development proceeds—witness the changes which occur in size, shape, and disposition of the nuclei, the appearance of vacuoles in the late stage—*pari passu* with changes in the arrangement of the blood supply.

YOLK.

The yolk masses at first occur in the granular ooplasm close to the zona; next they appear in vacuoles, cavities which are noted before the appearance of the yolk masses, and are later seen to become greatly enlarged and to be drawn together around the masses of yolk. The yolk itself increases in bulk, its masses now often presenting irregular protuberances, resulting apparently from a process of accretion. In surface view many of the yolk masses appear botryoidal (in eggs preserved in sublimate, acetic-sublimate, picro-sulphuric, picro-formalin). And this condition persists while the egg is attaining its mature size. In stages as late as gastrulation the coarse yolk differs little outwardly from the foregoing conditions. The grains show only a smoother surface and a possible tendency to coalesce; but it is evident that the vacuoles are now more closely adjusted to the yolk. The fine yolk, on the other hand, is, as Rückert's figures indicate in sharks, derived from the coarse yolk by a process of subdivision. Comparing the earlier stage (fig. 32) with one at fertilization (fig. 35), we observe that the substance of the former grains has become subdivided into morula-like masses of minute deutoplasmic elements, these, as before, lying in large vacuoles. In each of these masses one notes that there has usually been produced a globule of a highly refringent substance analogous to the oil-drop of the teleostean egg. In a later stage the corresponding portion of the egg has become a well-defined region of germinal yolk (Rückert's Keimdotter), and we are led to conclude that the later condition, with fine grains of yolk, is the result of a continued process of subdivision of the morula-like masses and their subsequent confluence. (The general character of the germinal yolk is shown in figs. 33 A and 33 B at *gy*.)

* In its latest stage the ovarian egg shows a series of capillaries (plate 11, fig. 5), converging to an elliptical stigma. Unfortunately, the relations of the tunic in this stage were not examined.

The grouping of the yolk elements in the mature egg is somewhat irregular. Sometimes "drifts" of germinal yolk underlie the coarse yolk; sometimes they extend obliquely, admitting between them inbursts of coarser yolk. In general, at the time of fertilization, the germinal yolk dips deeply down into the coarse yolk,

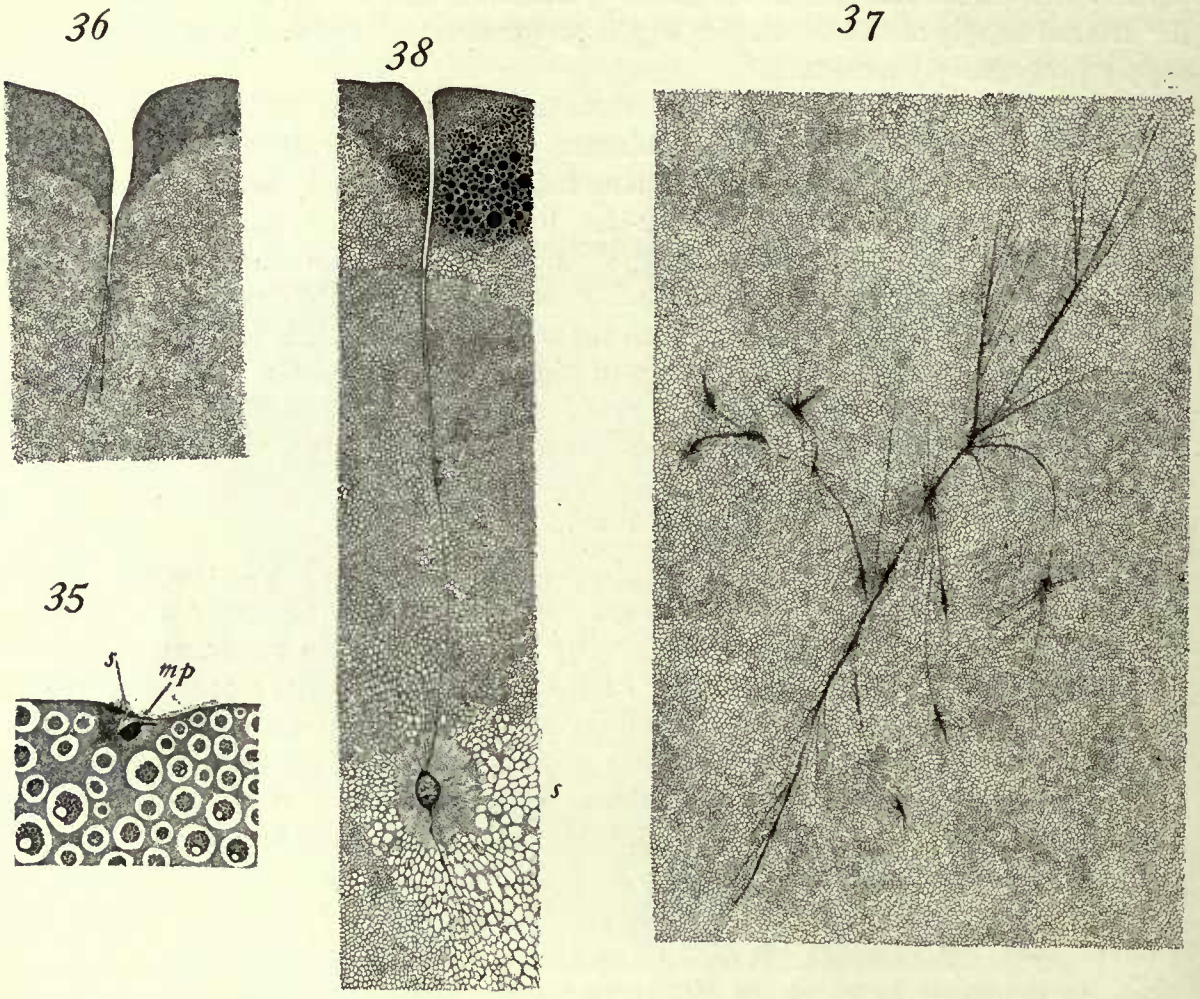


Fig. 35.—Section of fertilization stage, showing near the surface and at the side of the germinal area a sperm which has just gained entrance. This is shown at *s*, surrounded by a lighter area of germinal material. In the depression above the sperm is a mucus-like mass which may represent in part the tail of the sperm. *mp*, Middle piece. × 575.

Fig. 36.—Section of fertilization stage, showing deep entrance pit of a sperm. From the lowermost point arise branching rays.

Fig. 37.—Detail of section of specimen shown in fig. 34. From the path of a sperm astral rays branch in many directions, and at various points (indicated by the dark points) new centers of radiation appear.

Fig. 38.—Detail of fertilization stage shown in fig. 34. The present section follows almost exactly the entrance path of a sperm. The latter appears at *s*, and it is seen that the entrance pit is a delicate tube extending downward in the direction of a sperm. Around the latter appears a well-marked aster, and in this neighborhood, strung along a prominent ray of the aster, are a number of deeply stained "centrosomes." A similar "centrosome" occurs near the lowermost point of the entrance tube of the sperm.

forming a plug-shaped mass twice as deep as wide (fig. 34). This is possibly the homologue of the Panderian nucleus figured in the shark egg; certain it is, however, that the egg of Chimæra has not as clearly a marked series of tunics in its yolk arrangement.

THE GERMINAL VESICLE.

This is eccentric in eggs even as small as 3 mm. (*cf.* fig. 30). In the section of a well-grown ovarian egg shown in fig. 33 it lies close to the side of the egg. The spireme has here contracted into a minute mass and has given rise to (about) twelve pairs of chromosomes.* These are of remarkably small size, smaller by about one-half than those of a corresponding stage of shark (Pristiurus); and they are also smaller in terms of the germinative vesicle. In Pristiuris (Rückert) the mass of chromosomes at this stage measures 36 μ in width and the vesicle 296 ; in Chimæra

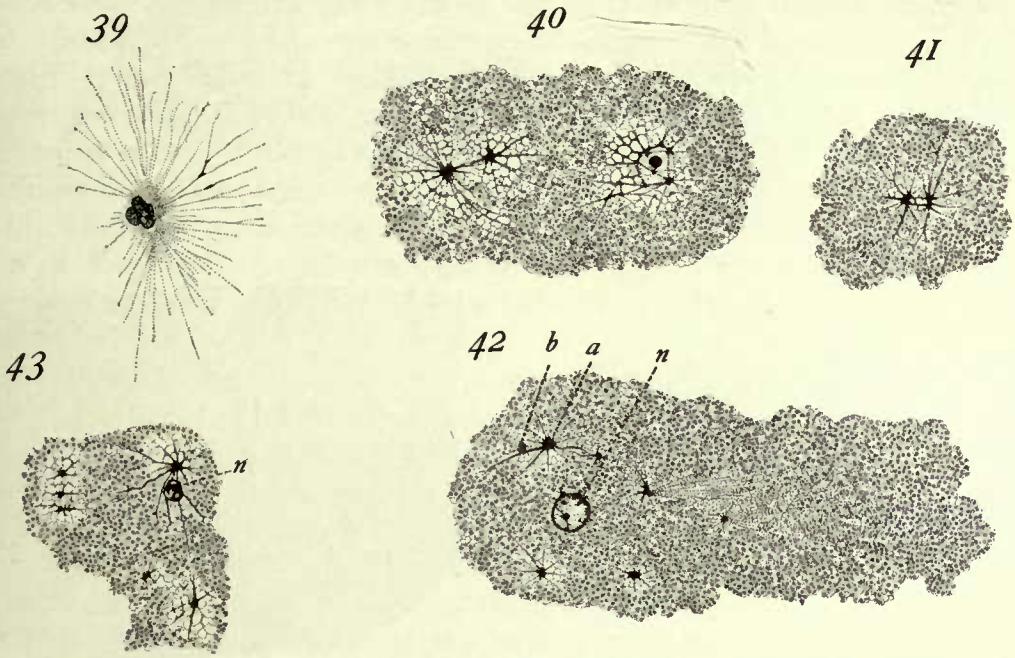


Fig. 39.—Detail of sperm nucleus from section of late fertilization stage. The sperm head is surrounded by a conspicuous aster, in some of whose dendritic rays appear the nodes referred to below. The sperm nucleus itself is undergoing amitotic division. × 475.

Fig. 40.—Detail of section of late fertilization stage. Throughout the germinal yolk occur asters which have no apparent reference to nuclear structures. At *p* many of these asters appear around a large granule of yolk. It will be seen that the rays are formed as lines in the thickened walls of alveoles.

Fig. 41.—Detail of section of late fertilization stage, showing asters in germinal yolk.

Fig. 42.—Detail of section of late fertilization stage. At *n* the egg-nucleus is shown surrounded by a number of asters. The asters appear to lack centrosomes and centrosphere. Note as before rays formed from rims of alveoles.

Fig. 43.—Section similar to the foregoing. A sperm nucleus, however (*n*), is shown surrounded by asters.

the same mass measures 16 and the vesicle 570. In other words, with a germinal vesicle twice the size, the size of the chromatin mass in Chimæra is but one-half that of the shark. In the shark the chromatin mass measures about one-ninth the diameter of the vesicle; in Chimæra, on the other hand, about one thirty-eighth. This condition indicates again the greater specialization in the egg of Chimæra. The chromosomes themselves, it will be remarked (figs. 33 C, 33 D), vary considerably in length ; thus the pair shown at x are apparently longer than those at y and at z, and a detailed examination has convinced the writer that this difference is a real one, *i, e.*, not due to the oblique position of the objects. This observation may be mentioned, since it affords an additional suggestion as to the individuality of the chromosomes, recently discussed, *e. g.*, by Sutton, Wilson, and Moenkhaus.

*Preliminary to first polar division. The number of chromosomes is clearly much smaller than in sharks (36 in Pristiurus and Torpedo).

FERTILIZATION.

Fertilization begins, as in sharks, in the uppermost portion of the oviduct and continues throughout the period of the formation of the capsule.* The earliest stage in the writer's material was obtained from a capsule like that shown in plate III, fig. 13, earlier stages not having been handled successfully. Late stages were secured

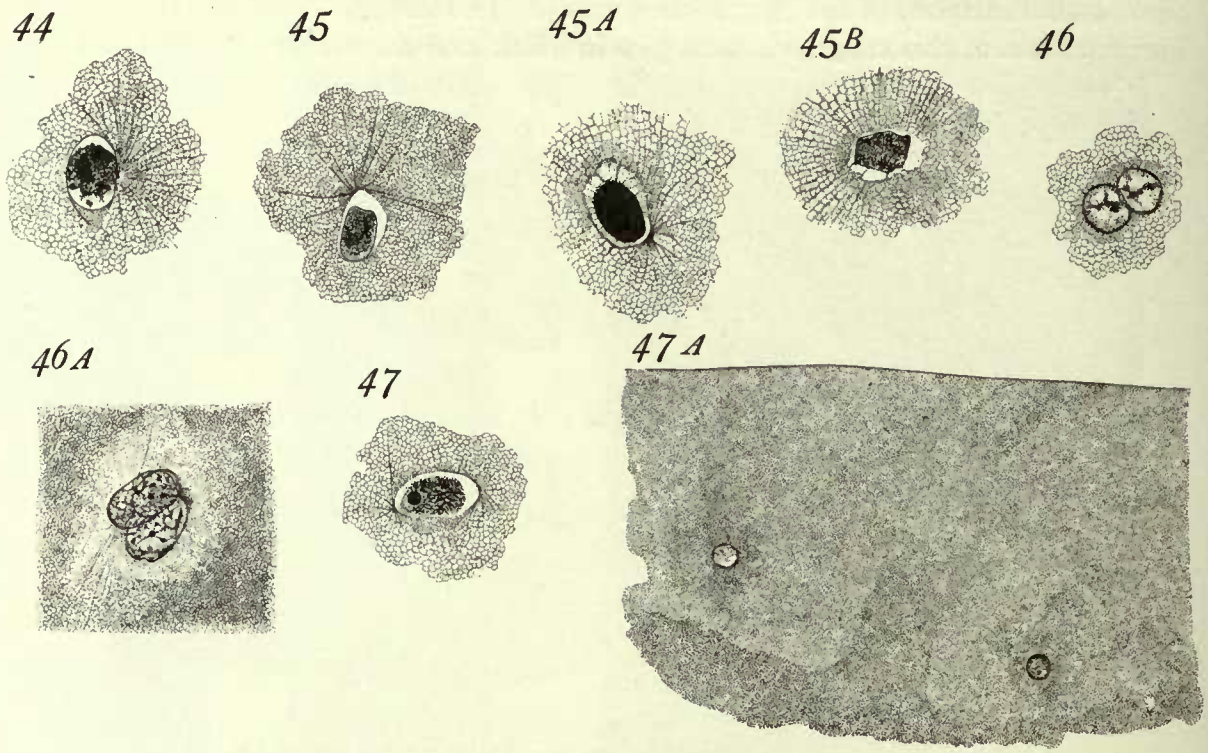


Fig. 44.—Detail of late fertilization stage, showing male nucleus in the process of approaching the egg nucleus. A club-shaped centrosome surrounded by astral rays appears at (right) side of nuclear membrane. × 475.

Fig. 45.—Detail of section similar to the last. A well-marked vacuole (artifact?) appears at one end of nucleus.

Fig. 45A.—Sperm nucleus with aster from section similar to the preceding.

Fig 45B.—Sperm nucleus from stage similar to foregoing. The center of aster is to be found in the section below present one.

Fig. 46.—Detail of section shown in fig. 34. Sperm nucleus has divided amitotically. This at first suggests a stage of copulating pronuclei.

Fig. 46A.—Egg and sperm nuclei in apposition. Rays not conspicuous.

Fig. 47.—Early prophase of segmentation nucleus. Two asters are present, one of which (the right) contains two centrosomes.

Fig. 47A.—Early segmentation stage. Section passing through segmentation nuclei. No surface furrows are as yet present. × 190.

from capsules about as shown in plate III, fig. 16. In the present account the stages may conveniently be referred to as early, middle, and late.

An early stage is shown in surface view in plate IV, fig. 18, magnified about 15 diameters. This was drawn from a living egg and shows the germinal area somewhat misshapen, due to rupture of the vitelline membrane.† The germinal area is not sharply outlined ; it is the same color as the remainder of the egg, and

* The egg at deposition is undergoing the first stage of segmentation.

† This is conspicuous at this stage, glossy and tense.

is only demarked by a slight furrow. Under a dissecting lens a number of minute depressions indicate the points of entrance of sperms. Seven of such points appear in the present instance, and all of them are peripheral; four are close together. In this case sections show that no sperms have entered the middle of the germ.

A middle stage in fertilization (plate IV, fig. 19), also examined in the living egg, showed 23 entrance pits. Of these half a dozen are of large diameter and several are minute, a condition which, in comparison with the preceding stage, suggests that the small pits are the early phases of the large ones, and we query, accordingly, whether in point of time the entrance of sperms in Chimæra may not prove an extended process (*v. infra*, heading *f*). In the present specimen it will be seen that the sperms have entered not only the germinal substance but the bottom and even the outer wall of the germinal fosse.

Study of sections leads us to conclude:

(*a*) That the tail of the spermatozoon does not enter the egg. In fig. 35 a sperm is shown which has just entered the egg; the middle piece, *mp*, ends abruptly, and there is no trace of the tail. The entrance pit is not yet sharply formed.

(*b*) That the head of the spermatozoon rotates as it travels inward. Even at the early period above figured, the filamentous character of the sperm head has been lost; it is now spheroidal, surrounded by a light-colored area of the germ. Although hardly within the egg, its axis inclines 45° to the surface, and its middle piece is parallel with the surface, a condition which by analogy with other forms leads us to conclude that it has already begun a process of rotation. In a later stage in the entrance of the sperm (fig. 38) the lighter-colored portion of the "head" points toward the surface of the germ and thus indicates that the rotation has been carried through an angle of 180°.

(*c*) A state of remarkable kinetic activity exists in these stages. In fig. 36 a series of "astral rays" are seen diverging downward from the entrance pit of a spermatozoon (*cf.* the observations of Miss Foote in Allolobophora). And from paths traversed by a sperm "astral rays" arise, sometimes radiating regularly, but usually branching irregularly and forming new groups of radiation. At such points of reradiation darkly staining bodies occasionally appear which remind one of centrosomes. In the present fig. 34 branching astral rays are seen. These, it is found, have arisen around a sperm path. A similar series greatly enlarged is shown in fig. 37, a series of considerable interest, since it shows many "centrosomes" surrounded by bending and irregularly branching rays. The "centrosomes" sometimes appear at centers of reradiating rays in sperm asters (figs. 38, 39); at other times they arise without any apparent relation to sperm asters or sperm paths, as around an unusually large yolk granule (fig. 40, the group at the right). As shown in the last figure, more than half a dozen centers of radiation appear around the yolk granule. On the other hand, the two large "asters" shown at the left in the present figure have no apparent relation with the former series, nor are they in the

neighborhood of sperm asters. A similar pair of "asters" are shown in fig. 41. On the other hand, the asters shown in fig. 42 are arranged around the male pronucleus, but how they are related to one another can not safely be inferred. In the following section (fig. 43), drawn from the same specimen, a similar radiation occurs around a supplemental sperm head, *n*. In the four preceding cases it is interesting to observe how perfectly the rays fulfil the alveolar conditions for aster formation as explained by Bütschli. Note in this connection the large size of the alveoli in the immediate neighborhood of the aster.

(*d*) The behavior of the germ nuclei in fertilization is similar to that in shark. The sperm which enters the germ in the region nearest to the egg nucleus is the one which accomplishes fertilization; it undergoes the customary form changes while traveling through the germ. In the stage shown in fig. 44 its chromatic material is becoming resolved, and the aster which appears beside it radiates from a centrosome, which is in this case somewhat elongated, situated close to the nuclear membrane. A stage somewhat earlier than the foregoing is shown in fig. 45; this, however, represents a stage in the development of a supplemental sperm head. The foregoing figures are taken largely from late stages in fertilization. A stage from a nearly finished capsule (fig. 46) pictures the union of the germ nuclei, *i. e.*, corresponding to Rückert's fifth stage in the fertilization of the ray (Torpedo), as figured in the Kupffer Festschrift (fig. 53 B). On the other hand, fig. 46 A, which at first sight suggests copulating pronuclei, must be construed as picturing a (sperm) merocyte dividing amitotically; for here a third nucleus is found to be present, above the niveau of the other two. The figure indicates, further, the retention of the aster and an extensive pale-colored area surrounding the nuclei.

(*e*) The behavior of the supplemental sperm heads is also notably shark-like. In even the middle stage of fertilization they can not readily be distinguished from the early sperm nucleus. Indeed, the nearer they are in a position to the egg nucleus the more difficult they become to distinguish from one another. And conversely those undergo the least conspicuous changes which occur in the margins of the germ. We have already referred, in fig. 45, to a structure which from its position is apparently the early sperm nucleus. In this phase, at the margin of the nucleus is a vesicular area, at one end of which an aster radiates from a minute centrosome. A somewhat similar appearance occurs in what, from its eccentric position, is undoubtedly a supplemental sperm head (fig. 45 A). Here the vesicular area of the nucleus is less perfectly developed, strands of karyoplasm passing from the nuclear membrane to the large and deeply staining mass of chromatin, a stage, indeed, which may be looked upon as the earlier condition of that of fig. 45. Another sperm head (fig. 45 B) from the same series of sections is intermediate between those of figs. 45 and 45 A. The vacuolated margin is now broken into several discrete areas, and the chromatin is collected into a diffuse mass, irregular in outline.* From this stage the transition is not wide to that of fig. 34, in

*The aster lies below the plane of the section.

which is pictured a (sperm) merocyte occurring eccentrically (*n*) in the germinal area of an egg twin to the preceding. In this the vacuolar area has been practically lost, the aster increased in size, and the nucleus subdivided into a number, probably five or six, of smaller merocytes. Division of this kind has been observed in many instances; and on the other hand no case has been found in which a sperm nucleus divides indirectly. This condition is noteworthy, since it emphasizes on still another line the specialization of the Chimæroid. For in the shark the sperm nuclei may undergo indirect division throughout practically the entire process of cleavage; and when early direct divisions do appear, *e. g.*, in the third cleavage (Rückert in Torpedo), they still show traces of their mitotic ancestry. Indeed, the nearest condition to the presegmentation division of the sperm head in Chimæra (fig. 39) occurs in shark only in the period of later segmentation (*cf.* Rückert, *op. cit.*, pl. III, fig. 18). In other words, the morphological (or the physiological) result which in the shark is effected only at the end of a series of graduated stages is accomplished by Chimæra at a single stroke—a condition worthy of comment, since it affords a palpable case of "precocious segregation."

(*f*) The sperms enter the germ not simultaneously, but during a relatively extended period. The pits formed by the sperms when entering the germ, as already noted, are different in size, and we accordingly infer that, as the sperms themselves do not differ materially in size, nor in all probability in individual activity, the difference in the pits is due to their having been formed at successive periods. This suggestion is borne out by examination of sections. Thus, in fig. 36 an entrance pit is shown, pointing down in the direction of, but not actually connected with, a sperm head lying deep in the germ. And here the pit or funnel has a wide mouth. On the other hand, in fig. 38, a funnel is pictured whose apex is still connected with a sperm head, and its mouth is narrow. The sperm head, in this case, lies in a shallower layer of the germ, and from its structure, also, is clearly a younger stage in development. It follows, therefore, that the former sperm entered the germ at an earlier period than the latter, and that the process of semination is a relatively extended one—relatively, since in sharks all sperms appear to enter simultaneously. The suggestion may, on the other hand, be made that the difference in the behavior of the sperms in the germ might be due rather to their location than to their time of entrance; or, in other words, that the rapidity of their development might be influenced by their proximity to the egg nucleus. This suggestion, however, is not tenable in view of the condition of the fertilization stage (middle stage) shown in plate IV, fig. 19, for here small pits occur side by side with large ones, both in the middle of the germinal area and on the sides.

Finally, to contrast Chimæra and shark in stages of fertilization: In Chimæra the entrance of the sperms is a protracted process; but as soon as the sperms (other of course than the one which fertilizes the egg) enter the germ they divide promptly by amitosis, with the very probable result of producing a greater number

of merocytes in a shorter time.* It thus appears that the early divided merocytes are equivalent morphologically, and probably, therefore, physiologically, to late merocytes in sharks. Furthermore, at the time of fertilization the number of sperms entering the egg of Chimæra appears to be greater than in sharks. The average number reckoned by Rückert in Pristiurus is about 16; in Chimæra it is at least 24, judging from the number of entrance funnels in late stages of fertilization. Again, in Chimæra the sperms form and long retain definite paths in the germ which are unknown in other forms; so also are their entrance funnels more conspicuous. The sperm nuclei, furthermore, as well as the segmentation nuclei, are the more special in terms of the entire egg, since they are smaller than in sharks (in diameter about one-half). Also, as evidence of specialization—for these structures have clearly a special physiological value—witness the great number of asters and their ready mode of appearance, *e. g.*, around vagrant yolk granules of extraordinary size. In point of histological differentiation of the germinal cytoplasm, finally, we observe in Chimæra conditions unparalleled in the shark. We recall here the differentiation of typical *Schaumplasma*, the light areas surrounding the nuclei, and the extensive development of astral rays.

SEGMENTATION.

Drawings of the living germ, plate IV, figs. 20–29, give a general idea of the process of segmentation. And in surface view this resembles distinctly the usual conditions in shark. There is the same type of germinal area in which cleavage lines appear, and a marginal zone which apparently circumscribes the area of cleavage.

In the first of these figures the germinal area appears convex, although somewhat flattened above, and is separated from the surrounding germinal yolk by a narrow fosse. The furrow which appears to traverse it is sharpest and deepest in the middle of the germ and fades away at the margins. The surrounding zone of germinal yolk, however, extends widely over the surface of the egg and lacks a sharply marked outer boundary line. Its inner boundary, *i. e.*, at the fosse, shows a number of small eminences These, as sections also show, correspond to the eminences formed in the shark blastoderm by peripheral (sperm) merocytes; they are more numerous at the corresponding stage and are more regularly disposed around the germ.

In further detail: Sections of the present specimen demonstrate that in spite of the single apparent furrow the present stage represents not the first, but the third cleavage, two cleavage furrows having been retarded (?suppressed), for there are found to be present six segmentation nuclei. This condition, it may be remarked, occurs in certain specialized sharks (Torpedo).

The first division of the segmentation nuclei is accompanied by no trace of a surface furrow. Such a stage is shown in fig. 47 A. The nuclei are here somewhat widely separated from one another and are in the resting stage; the only indication

*Recent examinations of the sections of the fertilization stage which yielded fig. 46 A (Chimæra Emb. 12, in my cabinet) show that no less than 88 (sperm) merocytes are present. Thus in Chimæra as many merocytes are present in a presegmentation stage as in Torpedo (Rückert) in a stage of fourth cleavage.

of cleavage is in the arrangement of the germinal cytoplasm around the nuclei. This is expressed in such a way that the germinal yolk rises between them like a wall.

The second stage in which cleavage is seen at the surface is shown in plate IV, fig. 21, from the egg companion to the one shown in plate IV, fig. 20, but incubated longer (about forty minutes). Here a second furrow is noticeable. The resulting "blastomeres" are unequal in size, one of them being as large as two of

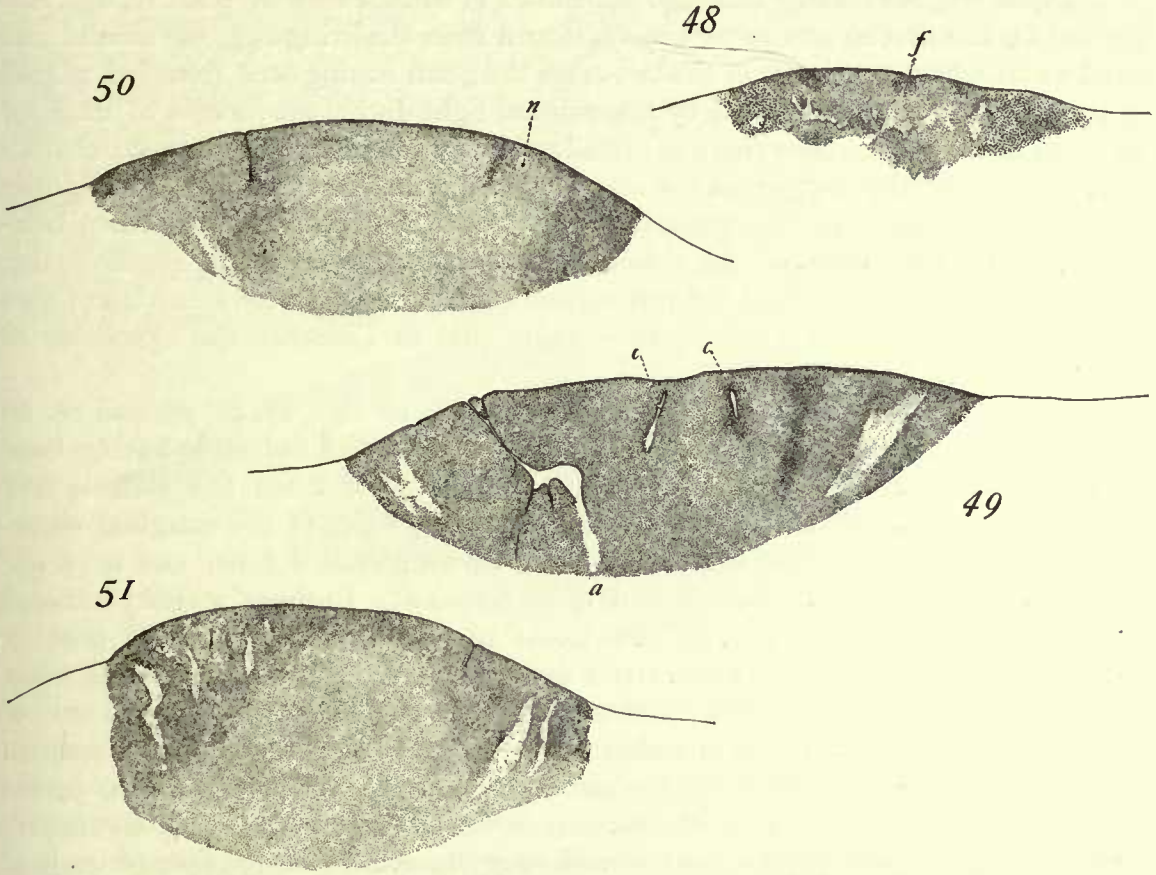


Fig. 48.—Section passing between the point 1 and 1 of the segmentation stage shown in Pl. IV, fig. 20. In the present section the line which appeared to indicate first cleavage lies below the point *f*; below this a vacuole is present whose lateral extent gives one the impression of the width of the furrow noted in surface view. × 35.

Fig. 49.—Section through a segmentation stage corresponding to Pl. IV, fig. 22. It will be observed that some of the cleavage lines do not open to the surface, as at *c*. On the other hand, one of the spaces between the blastomeres opens into a fissure-like vacuole, *a*.

Fig. 50.—Similar section of early segmentation stage, in which, as at *n*, a nucleus appears without any neighboring cleavage furrow. A line of thicker germinal yolk appears in its place.

Fig. 51.—Section of early cleavage stage in which, when viewed from the surface, deep, fissure-like vacuoles appear as cleavage lines.

the others. As in the companion stage the furrows fade away at the margin of the germinal area, and this is again surrounded by a somewhat regular ring of merocyte eminences. It may be mentioned that these characters are materially modified, *i. e.*, as far as surface view is concerned, when the egg is hardened, *e. g.*, in acetic sublimate. And in sections it is found that the circumgerminal fosse and merocyte eminences disappear and what was interpreted as surface furrows in the living egg appear as long and wide vacuoles. Thus in fig. 48, a section transverse to the

first cleavage line of the stage of plate IV, fig. 20, the fosse will be seen to have disappeared, and the line which indicated cleavage, so conspicuous in surface view, now appears under the point *f* as a vacuole triangular in section, its apex touching the surface of a germ.* Vacuoles, we note, are abundant in early stages; several are present in the section of the germ just referred to, and from their arrangement they suggest the division of the germ into blastomeres.

Three stages of early cleavage are shown in surface view in plate IV, figs. 22, 23, and 24, the first as an opaque object, drawn from the living egg, the second and third as translucent objects, in the last cases the germ having been removed, placed in a watch glass, and examined by transmitted light during the process of fixation. In these three preparations there is considerable irregularity in the surface characters; in the first the margins of the blastomeres are rounded, in the others angular; outwardly they appear to represent fourth and fifth cleavages; in section, however, single "blastomeres" are sometimes found to contain several segmentation nuclei. It was observed that the resting and dividing nuclei were sometimes found in the same section, and it follows accordingly that in Chimæra the synchrony of cleavage is early lost.

Four later stages of segmentation appear in plate IV, figs. 25, 26, 27, and 28, all drawn under conditions of transmitted light, the living specimens having been removed and examined in watch glasses. In the first of these the germ is well marked off from its circumgerminal zone; in the rest some of the marginal cleavage lines were traced half-way across the circumgerminal zone, and in a few instances these lines could be followed quite across it. In these stages continued subdivision of the "blastomeres" has taken place, those in the central position becoming divided oftener than those near the periphery. As in earlier stages, some of the cleavage lines are probably not expressed at the surface, and are due only to vacuoles; the latter are lineal in surface view, sometimes wide, sometimes narrow, occasionally almost attaining the surface, at other times lying fairly deep in the germ. (*Cf.* figs. 49, 50, 51.) Sometimes, as in fig. 49, they are actually continuous with cleavage furrows, as at *a*, and considering the relation which they often bear to nuclei (*e. g.*, *infra*, under the heading "gastrulation"), we conclude that in some cases—even, indeed, in many cases—they are homologous to cleavage spaces, *i. e.*, that they are cleavage spaces which fail to become expressed at the surface of the germ. This conception appears to be applicable even when the vacuoles appear in the peripheral region of the germ in fertilization stages. Thus in fig. 34 the masses of germinal yolk separated by the vacuoles (under the points marked with an asterisk [*]) usually bear sperm nuclei which, as we know by analogy, will cause "segmentation." Accordingly, even in this position vacuoles may be compared to intercellular spaces, at least from the standpoint of developmental mechanics.

In fig. 52 a section of a segmentation stage corresponding to plate IV, fig. 26, shows that cleavage has by this time extended deep into the germinal area. Horizontal divisions have occurred, irregularly however, for in some places the blastoderm

*There is thus a possibility of there having been an open furrow in the living egg.

varies in thickness from one to five cells. Noteworthy is the irregularity of the yolk wall out of which blastomeres are segmenting, as at *x*, and into which deep intercellular spaces are continued, becoming confluent below, as at *v*, *v*, *v*, with vacuoles like those described in earlier stages. It may be remarked that in this stage the vacuoles pass deeply into the yolk.

Another stage of late segmentation (or blastula), corresponding in general with plate IV, fig. 27, is shown in the series of sections, figs. 53–56. In the section, fig. 53, which passes near the center of the germ, the conditions differ little from the preceding stage. We observe that continued divisions have taken place and that there is still the same outcropping of blastomeres from the yolk wall, as at *x* and *x*, following mitoses. An advancing character in this stage is the general flattening of the germinal wall, as at the point *y*, a preliminary step toward the formation of the floor of the segmentation cavity, and possibly indicating fore and aft differentiation of the germ. It may be remarked that this is the first stage in which a conspicuous zone of merocytes was seen. These are numerous under the central blastomeres, most numerous under the peripheral blastomeres, and then rapidly decrease in

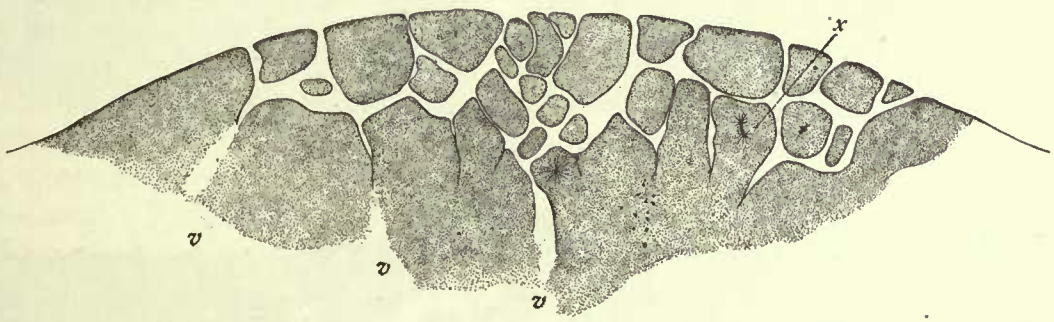
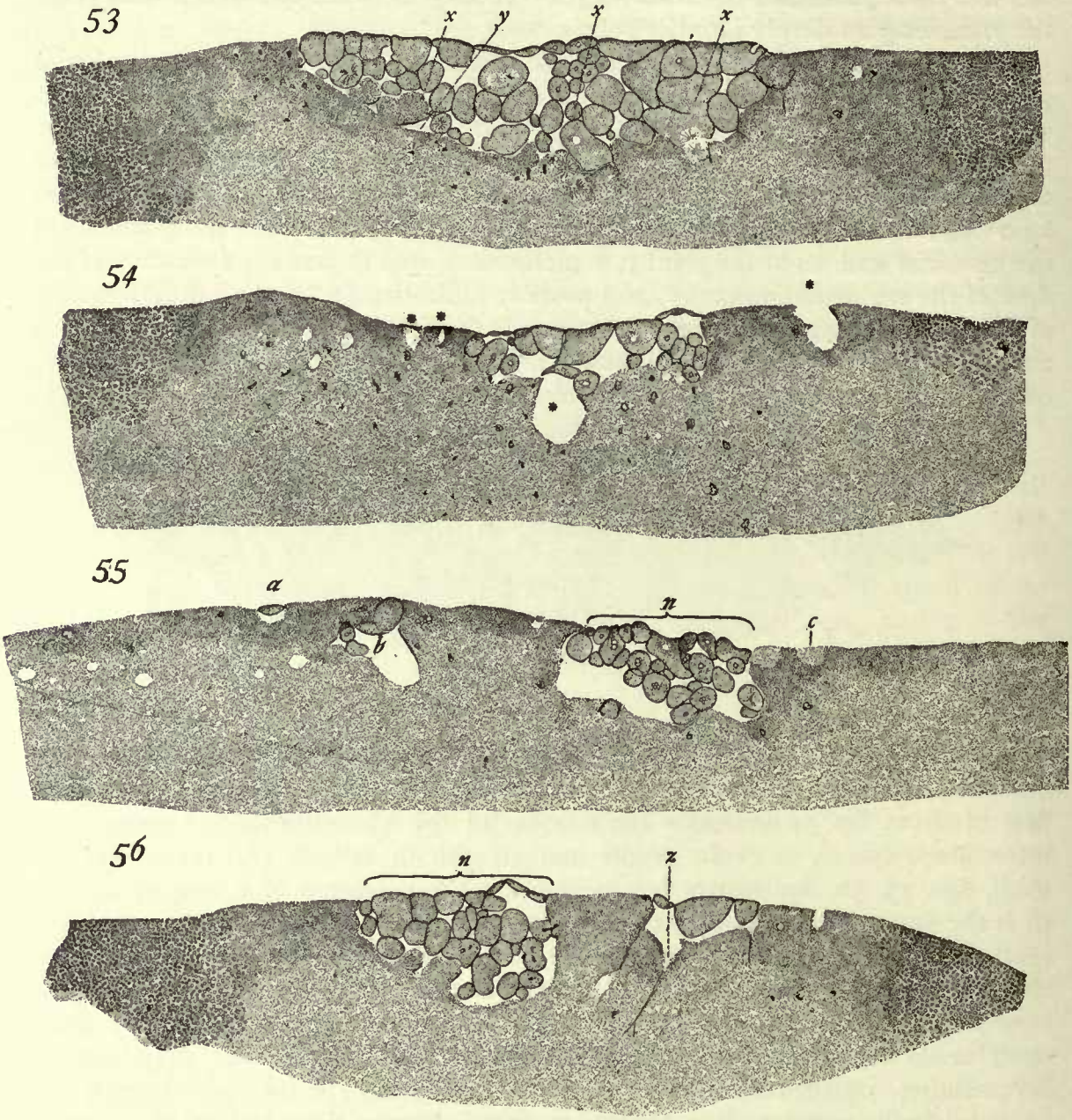


Fig. 52.—Section of late cleavage stage (corresponding to Pl. IV, fig. 26). *x*, Mass of germinal yolk from which a blastomere is being budded out; *v*, vacuoles which are continuous with intercellular spaces.

number peripherad. The three sections, figs. 54–56, illustrate such a series. The first of them, fig. 54, indicates the relation of the above-mentioned vacuoles to intercellular spaces, as at the points marked with an asterisk (*); the second and third, figs. 55, 56, are instructive as showing the extension of a nest of cells, *n* (it is the same group in both sections—it appears, however, at the left in the lower section, since this has been turned over on the slide), beyond the margin of the circular mass of blastomeres—instructive, since it suggests that the outlying region of the germ (circumgerminal zone) is still little different from the germ itself in its cell-forming nature. It is also to be observed that deep fissures representing intercellular spaces (fig. 56, *z*), extend peripherad through the germinal yolk, corresponding to the marginal furrows described in the eggs of ganoids and dipnoi, of Heterodontus, even of amphibia. There is here accordingly a region in which, side by side, occur small blastomeres, large yolk masses (bearing nuclei), and undivided yolk; there is no gradual transition from the yolk to the large blastomeres and from these in turn to the small ones, which, as we have seen, correspond in size with blastomeres of the center of the germinal area. We observe, furthermore, that the small blastomeres arise in any

neighboring position, as in figure 55, at *a*, *b*, or *c*, budding out directly from the yolk. In such cases the important question remains whether the nuclei which pass into the blastomeres are derived from segmentation nuclei or from



Figs. 53–56.—Sections of late segmentation or early blastula stage (corresponding to Pl. IV, fig. 27). The first section traverses the mid-region of the segmented area, the others progress marginalward. *x*, Blastomeres which have recently budded out of the yolk; *y*, wall of sub-germinal yolk; *z*, cleavage line passing deep into the sub-germinal yolk; *, vacuoles which come to the surface of the germ and form intercellular spaces. × 35.

sperm-nuclei. In the latter event, judging by analogy, they would show amitoses only; in the former they should multiply by mitosis. Examined in this light it is found that the nuclei which here pass into the blastomeres show amitoses, and

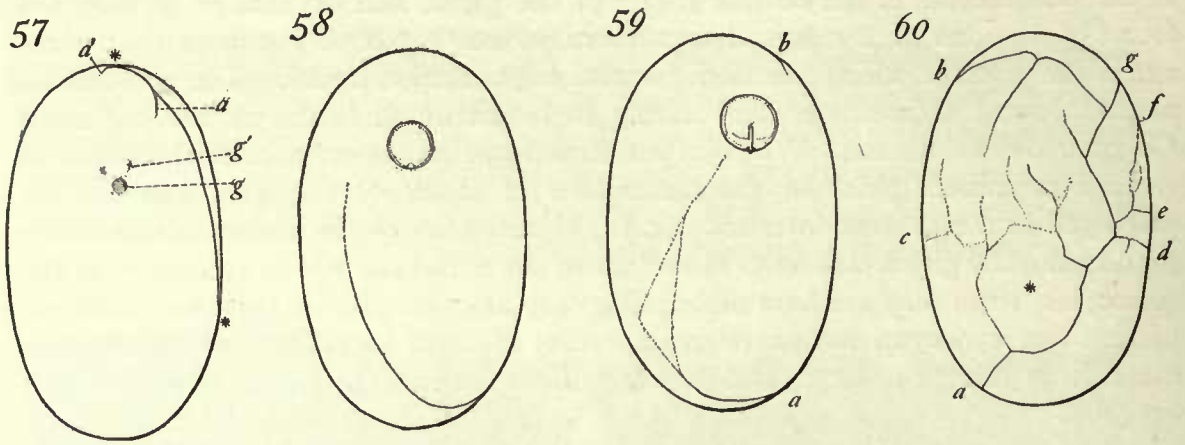
they might thus be regarded as of sperm-head origin. On the other hand, it might still be claimed that the nuclei of such blastomeres were derived from the segmentation nuclei, for a more careful examination shows (1) that amitoses exist in the blastomeres in the central region of the germ, and (2) that no mitoses are found in the zone of the merocytes, where we may reasonably expect that some nuclei are present which are derived from segmentation nuclei. The problem is, nevertheless, a difficult one, and hardly to be answered in the present outline of Chimæroid development. We point out, however, that two criteria which have been given a prominent place in the discussions of shark development can not be employed in the present instance, viz. (1) the number of the chromosomes which would naturally give a clue as to the origin of the nuclei can not be estimated in the merocytes, since they are here undergoing only amitotic division; (2) the size of the present merocytes can not prove an important element for comparison, since they range from minute to large, and in shape from spherical to greatly elongated and irregular.

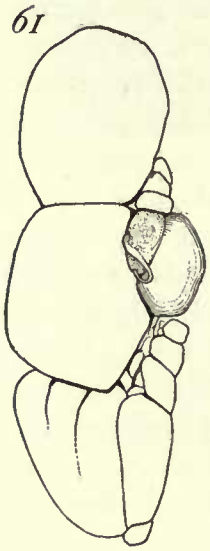
An important phase of the cleavage in Chimæra has naturally been introduced by the foregoing discussion, *i. e.*, as to the segmentation of the egg in its extra-germinal region. We have seen that as segmentation progresses nuclei (whether segmentation or sperm-merocyte) spread peripherad. Their presence can be determined in sections ; and in surface view, in the later stages, *e. g.*, plate IV, fig. 28, cleavage lines can be seen passing outward in the region of the circum-germinal zone. That these lines are actual furrows is shown in such a section as that of fig. 56 (at the right). Such marginal furrows, however, are usually minute in size, and are often, in surface view at least, difficult to follow, a difficulty which may be due either to the blending of these delicate lines with the color of the circumgerminal zone, or to the partial or total confluence of the adjacent rims of the cleavage furrows, *e. g.*, as in the marginal blastomeres of Cryptobranchus (according to Ishikawa). The distinctness of these lines, however, increases after the circumgerminal zone is passed, and they later give rise to what we must regard as the most remarkable feature of the segmenting egg.

To follow this process: In fig. 57 a late stage of segmentation is shown; the germ is at *g;* nearby are nests of blastomeres (*cf.* fig. 56, *n*), two of which are of such size as to appear in the figure, as at *g'*; from the germ radiate furrows, two of which, *a* and *a'*, have become conspicuous at the periphery of the egg, where they may have merged with similar furrows, or indeed, on the other hand, there is a possibility that the long furrow passing between the points marked with an asterisk (*) may be the deflected continuation of the lines *a* and *a'*.

In figs. 58 and 59 furrows are seen arising from or near the circumgerminal zone, and examination shows they deepen as they proceed peripherad. In the egg shown in fig. 59 the outgoing line subdivides and marks out superficially a narrow segment of yolk. In the same egg, but in the anterior region, we note another marginal line, *b*. Examined from below this stage is of considerable interest

(fig. 60), for it shows that while the cleavage lines have failed to express themselves on the dorsal side of the egg, they yet appear conspicuously on the vegetal side. Thus the line in fig. 59 at *a* passes sharply inward (fig. 60), subdividing into a series of





Figs. 57–61.—Eggs showing progressive cleavage of the yolk mass. In a blastula (57) a conspicuous fissure is noted between the points * and *.

cleavage lines which in turn merge with other cleavage lines (*b–g*) passing downward and inward from the equatorial zone of the egg. In some cases well-marked yolk masses are outlined, as at the point marked with an asterisk (*), suggesting large yolk-filled blastomeres on the ventral wall of an amphibian blastula. It may be remarked that the lines here described are not mere surface markings, for during the process of hardening an egg, *e. g.*, in acetic-sublimate, one may separate the yolk masses by aid of dissecting needles, and in this process it becomes clear that the lines are in reality fissures dipping deeply into the substance of the egg. Indeed, in the former specimen it was found that the mass marked with an asterisk (*) could be removed *en bloc* from the remaining mass of yolk. It is evident, accordingly, that in this stage the egg is being divided up on its ventral side into a number of large yolk masses; that these masses stand in relation to the entire egg very much as do, *e. g.*, in the frog's egg, the blastomeres of the lower pole to this entire holoblastic egg; further, that the fissures which accomplish this result, like cleavage lines on the vegetal side of the holoblastic egg, are interconnected with a series (*a–g*, in fig. 60) of cleavage lines which pass downward and inward from different points in the equatorial region of the egg. Between the stages shown in figs. 59 and 60, and those in figs. 61 and 27, which are older by about nine days, observations are lacking. It is nevertheless clear, by comparison of these stages, that the yolk masses shown in fig. 60 have separated from one another widely as the fissures deepened, and that, as the masses became more distinct, their condition of surface tension—in view always of the syrupy consistency of the egg—caused them to round out their contours to the degree shown in fig. 61.

In dorsal view the latter stage shows few large yolk masses, and these are distinct from one another, although closely pressed together. The yolk masses, it may be mentioned, were removed separately (in the living condition) without causing their rupture, and it was then seen that the fragmentation of the yolk mass had progressed further than was at first evident, for, lying below and on either side, against the ventral wall of the capsule, were many small masses of yolk (*cf.* fig. 61, at the right, and fig. 27, somewhat behind the embryo), their contours rounded out for the most part; but a thick, creamy or syrupy fluid in which they lay made it further evident that in some cases the yolk masses had broken down. This fluid, we remark, was observed in specimens of this stage only when the larger masses were separated; but if sea-water was injected (by pipette) between the larger masses as they lay in the open capsule, it would dissolve the underlying creamy yolk and the entire contents of the capsule would become hidden from sight in the resulting milky fluid.

One might conveniently digress at this point to follow the fate of the yolk masses above mentioned. The blastoderm appropriates only a small portion (which has been estimated as about one-tenth of the volume) of the entire egg. This separate yolk mass is shown slightly shaded in figs. 27 and 61, and the blastoderm, with its attached embryo, has as yet inclosed only a small portion of it. A similar stage is figured in plate VIII, fig. 47, and a somewhat later one in plate VIII, fig. 48. In the latter the blastoderm is seen to have almost inclosed the yolk. It completely incloses the yolk and forms a diminutive yolk sac in the embryo shown in plate VIII, fig. 49, and a similar condition occurred in the embryo of plate IX, fig. 50. These features are dwelt upon in order to show that the behavior of the blastoderm in appropriating but a portion of the yolk is a normal phenomenon. And I note that the condition shown in fig. 61 has been observed on three occasions by myself, and that similar conditions were recorded by Dr. Wilbur.* In supplementary evidence upon this point we may again refer to the embryo of plate VIII, fig. 49, for in this the yolk sac, although of miniature size, is evidently normal, since it exhibits a well-developed vitelline circulation.†

The yolk-masses other than that appropriated by the blastoderm undergo continued subdivision. This is in progress in fig. 61, where the large yolk mass shown in the lower part of the figure is being divided into three smaller ones. We have already referred to the pasty fluid present among the lowermost yolk masses in this stage. In the egg capsule from which the embryo of plate VIII, fig. 49, was taken, no extra embryonic yolk masses were found, but the egg capsule contained a fluid so cream-like as to conceal completely the embryo and lead me to infer that the egg was addled, almost causing me to throw away this valuable stage. We can only conclude, therefore, that the creamy fluid was due to the continued breaking down

*In his early letters Dr. Wilbur referred to these conditions doubtfully; he was then "not sure whether they represented normal appearances."

†The yolk sac measured about half an inch in length and a quarter of an inch in breadth; accordingly at this stage of development it represents but about one-tenth the volume of the egg of an Elasmobranch of similar size (*e. g.*, *Spinax niger*).

of the yolk masses of the earlier stage.* That this fluid was nutritive to the embryo was also evident, since the external gills were dilated at various points with brilliantly colored blood knots, and in these, as I later found, numerous erythrocytes were undergoing division. And this condition in the gill filaments is the more clearly correlated with the presence of the milky fluid, since in similar egg capsules (sharks and rays), where this milky fluid mass is lacking, blood knots on the external gills are also absent. One infers, moreover, that the milky fluid, which from its included yolk is highly nutritive, may also be passed as food into the mouth of the embryo and assimilated in the gut. But to this I will refer at a later point.

The entire process of the fragmentation of the egg of Chimæra, it will be seen, is worthy of especial comment. Unlike the eggs of other vertebrates, and unlike, indeed, those of invertebrates, unless we include a somewhat generic resemblance in certain mollusks (*e. g.*, Neritina, Blochmann, 1887) and in certain digenetic trematodes, the present egg follows in its development two distinct paths, *i. e.*, a small portion of the egg develops in the direction of producing the embryo with its complete though diminutive yolk sac; the remaining portion, about nine-tenths of the bulk of the egg, proceeds to undergo a process of repeated fragmentation to the end that it may be appropriated by the embryo secondarily.

To account on phyletic grounds for this extraordinary and "unnatural" plan of development, one must, I believe, start with the premise that the fragmentation of the egg is a process comparable with total cleavage. This premise we may accept on the following evidence:

(1) The fragmentation, like cleavage, is progressive.

(2) Although the cleavage lines have never been followed conclusively from the rim of the blastoderm into the deep fissures which initiate the fragmentation, they have at least been observed in late stages of segmentation to pass out over the circumgerminal zone in the direction of the peripheral fissures (*cf.* in this regard the evidence of Heterodontus).†

(3) The yolk masses give evidence of being nucleated. There is in the first place evidence that the nuclei travel peripherad. In the stages of plate IV, figs. 25–27, nuclei are found to have occupied the circumgerminal zone, *i. e.*, they have traveled outward a distance equal to about three-quarters of the diameter of the blastoderm. In an early gastrula, furthermore (plate V, fig. 31), and in section, fig. 63, they have proceeded outward a distance equal to twice the diameter of the blastoderm. Now, on the evidence of progressive centrifugal movement of the

*The reader may reasonably query at this point how it happens that the creamy nutritive material is not washed out through the openings of the capsule during the respiration of the young. This result has, I take it, been avoided in the course of the evolution of this process in two ways: (1) By retarding the appearance and growth of the capsular openings until the nutritive material is partly consumed; (11) by the great density of the creamy fluid, for if the nutritive fluid be heavy (and experiments with the living eggs have convinced me that this is the fact), a moderate current of sea-water could be passed over it without causing it to be washed away.

†Annot. Zool. Jap., 1901, vol. IV, pt. 1, pp. 1–7.

nuclei, and as this nucleated area (in diameter) is measurably greater than that of the yolk mass which the blastoderm comes to inclose, it follows that nuclei are present in some of the outlying yolk masses. Of this, however, we must none the less admit that no direct proof is at hand, since no sections of these outlying yolk masses were made. In this connection I observe that if the embryo-bearing yolk mass be examined even under a low power (plate VIII, fig. 48*a*) one obtains a fairly convincing picture of its holoblastic character.

(4) The foregoing evidence is none the less strong if, conversely, we consider that on no other morphological ground, save that of cleavage, using the word in a broad sense, can this progressive and normal fragmentation be explained.

Accepting, then, the premise that these divergent paths in the development of the egg of Chimæra took their origin in a holoblastic egg, the present conditions may well have been developed on somewhat the following lines: In the primitive Chimæroid the egg resembled that of Cestraciont; it was probably, however, not as large as that of the recent Heterodontus, but its cleavage fissures were deeper and more numerous. The embryo at that stage had the usual external gills of the selachian. The next stage would be attained when the gill filaments, passing beyond the stage of the well-known trophonemata, came to appropriate the white of the egg which was contained in the deep cleavage fissures, a process which in time caused or accompanied (*a*) the deepening of the fissures, and in further time (*b*) a rupture at the bottom of the fissures. Through such a process yolk material came to escape and mingle with the albuminous contents of the deep fissures. Such a process, we may now assume, was naturally followed by adaptative changes in the trophonemata, which in the end accelerated the growth and differentiation of the embryo. In short, at this evolutional stage the embryo was receiving through a (morphologically) indirect channel an amount of nutriment which rivaled that derived from the vitelline circulation. The result was what one would have anticipated, *i. e.*, the down growth of the vascular blastoderm was retarded, while the fissuring of the yolk-mass became deepened and the trophonemata further modified. The line of evolution thus carried on in the egg will be seen to involve the fate of the yolk sac, viz., in determining how great an amount of the yolk could be diverted from it. In the present species (*C. colliei*) about nine-tenths of the egg has been diverted, while in the Callorhynchids, where the yolk sac is known to be larger, possibly not more than half.

In the foregoing process it is suggested that the first steps in the disintegration of the yolk mass were found in cleavage phenomena. It should, however, be admitted that the cleavage may not have been equivalent to that of the usual holoblastic type. The nuclei which spread peripherad may have been sperm-nuclei; and in this event the peripheral furrows are special phenomena, unconnected, possibly, in phylogeny with the cleavage lines in the holoblastic egg. Certainly in favor of such an interpretation is the fate of the disintegrating yolk masses, since such a fate is paralleled somewhat by the sperm-nuclei in the shark egg. It

is opposed, on the other hand, by the conditions in the egg of Cestracion, where the peripheral furrows, similar in general regards, are known to be continuous with those of true cleavage. The question, therefore, can not be answered finally until evidence is forthcoming to distinguish the kinds of nuclei present in the extra-embryonic yolk masses. Meanwhile, judging at least from the behavior of the nuclei in the circumgerminal ring, I think it is not at all improbable (*cf.* Gastrulation) that in these masses both sperm and segmentation nuclei are present.

Returning again to the development proceeding at the animal pole of the egg:

We recall that in the sections figs. 53–56 there was shown a stage of late segmentation, or an early blastula, such, for example, as pictured in plate IV, fig. 27. In a slightly later stage (plate IV, fig. 28) an increased number of blastomeres are present, and there is still an indefinite condition in the periphery of the germ, blastomeres being continued irregularly over the ring-like circumgerminal zone. On the other hand, in plate IV, fig. 29, a stage is figured earlier than the preceding,

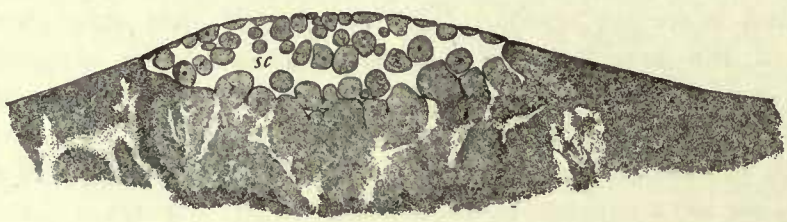


Fig. 62.—Section of blastula. *sc*, Segmentation cavity.

but showing a well-marked line of demarcation between the blastomeres and the circumgerminal zone. It seems evident, accordingly, from this and similar instances, that considerable variation occurs as to the time at which the marginal relations of the germ are established. Thus in the stage first referred to (figs. 53–56) the circumgerminal zone was traversed by radial fissures and invaded by nests of cells; in a similar stage (plate IV, fig. 29, sectioned in fig. 62) the same region is solid and yolk-filled, forming a compact border to the germ.

In contrasting these two stages one observes that, while they can differ little in point of age, judging from the number of blastomeres in the cross section of the middle of the germ, they yet have marked differences in their relation to the yolk; the former has around it and under it "fine yolk" (Rückert); the latter has its fine yolk contracted into a thick mass lying immediately below the germ, a condition which may be the immediate cause of the failure of marginal blastomeres to express themselves in a peripheral direction. We observe that in fig. 62 the fine yolk is pervaded with vacuoles which, from their shape and relations, are evidently equivalent to inter-blastomeral spaces, a conclusion which is supported both by the nucleated character of the masses of fine yolk thus outlined and by the continuation of the inter-blastomeral spaces with the distal ends of the vacuoles. The fine yolk, in short, is already coming to be formed into blastomeres, and it is interesting to note that a blastomere, which is found on the boundary line between the fine

and coarse yolk is composed half of fine and half of coarse yolk. It is quite probable, therefore, even from this single observation (*cf.* also *infra*), that the region of the coarse yolk is not as inert as one is at first inclined to believe, an induction which suggests at once that the fewer and larger fissure-like vacuoles in this region are equivalent to the vacuoles of the fine yolk, or in other words, to intercellular spaces.

A final point of contrast between the foregoing stages: In the former the blastomeres are relatively compact; in the latter there is a general inter-blastomeral space which marks an early state of the definite cleavage cavity. It is probable, as noted for the former stage, that the anterior end of the germ can now be distinguished.

GASTRULATION.

The stage shown in surface view in plate v, fig. 30, and in sagittal section in fig. 63, is probably the most valuable of the author's early Chimæroid embryos. For it may be accepted as providing a key to the problem of gastrulation not only in this form but in sharks as well. Its discovery is none the less a fortunate one, since it is a stage which has every appearance of being brief, and therefore easily overlooked. In diameter it differs little from the blastula above described (fig. 62), but its depth is notably greater. Comparing these two stages, we conclude that the deep subgerminal region of the earlier stage (fig. 62), which was traversed by vacuoles, has been replaced by the deep-lying mass of cells of fig. 63. We observe that this thickening of the cellular mass has not yet been accompanied by an extension over the surrounding region; the mass is at present compact, subspherical, lying in a smooth depression of the germinal wall. At one end of the cellular mass the segmentation cavity, below the letters *sc*, represents all that remains of the intercellular spaces of earlier stages. Near the opposite end is a small archenteric cavity, *a*, communicating with the surface through the opening *bp*. The archenteron is regular in outline, its marginal cells forming a somewhat epithelial lining (fig. 63 B). It has probably arisen by an invagination in preexisting cells, since the cells lining its outer half are slightly pigmented and closely resemble those of the surface of the blastoderm. Especially noteworthy is this—that behind the archenteron, *i. e.*, between it and the germinal wall, are several rows of cells.

We have, therefore, evidence that in Chimæra a gastrula is formed whose blastopore is located not *at* the rim of the early blastoderm but *near* it. *It is thus a condition in which the merging of the cells of the blastoderm with the surrounding yolk does not yet take place in that zone of the blastoderm in which the archenteron is forming.* We have here, accordingly, a condition which throws light upon the origin of the gastrula of sharks, confirming in a striking way the interpretations of C. K. Hoffman (1896, Morph. JB., p. 210).

Continuing our examination of the present specimen, it will be observed that the growth of the cell mass is taking place at both anterior and posterior margins. Cells are still being contributed to the cellular wall behind the archenteron, judging at least from their relations to the yolk—such a blastomere, for example, as that near 2 having become detached from the germinal wall. And at the extreme anterior region of the blastoderm many cells are being budded out of the germinal wall. Thus, as shown in the detail (fig. 63 A), it will be seen that in an overhanging portion of the germinal wall, as below and between the points marked with asterisks (*), a row of half a dozen cells are clearly outlined in the wall—a condition which indicates strongly a similar origin for the adjacent cells. At lower points of the

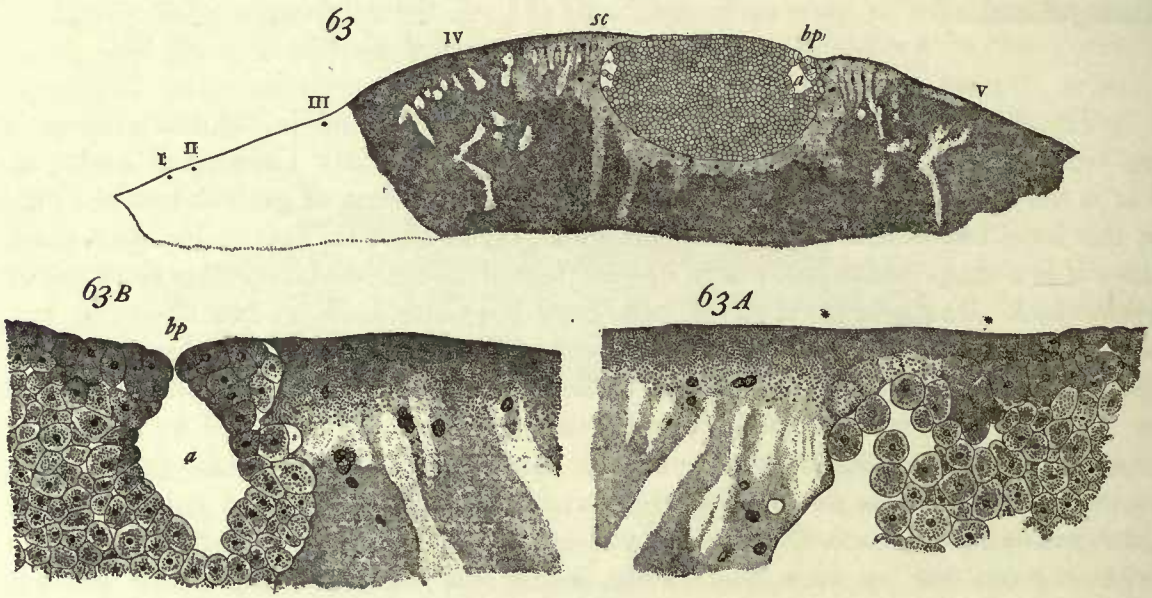


Fig. 63.—Sagittal section of earliest gastrula. *a*, Archenteric cavity. *bp*, Blastopore. *sc*, Segmentation cavity. I–V indicate position of nuclei in yolk region.

Figs. 63 A and B.—Details of foregoing section at anteriormost and posteriormost margins respectively.

germinal wall, finally, cellular additions to the blastoderm are being made. Noteworthy in the present section are the vacuoles which pass deeply into the yolk and suggest, as we have already noted, modified or suppressed lines of cleavage; especially well marked are those occurring in the fine yolk on either side of the blastoderm, since they form a series of vertical fissures and mark off masses of fine yolk containing nuclei. The vacuoles also occur throughout the neighboring coarse yolk, and in connection with their appearance there we note the presence of merocytes which have traveled, as at IV, III, II or I, far out over the yolk. We note, lastly, the way in which the fine yolk passes down in rifts into the coarse yolk, for this suggests again the modified holoblastic condition of the egg.

The next stages in gastrulation deal with the extension of the blastoderm over the yolk. Thus in fig. 64 is given a sagittal section of a stage in which the diameter

of the blastoderm has doubled and during this growth it has lost the compact character of the earlier stage. We recognize, however, in the cellular mass (at the left in the figure, *pm*) the group of cells which formed the ventral lip of the blastopore, and from a detail of this region, fig. 64[I], we conclude that the blastopore, *bp*, has

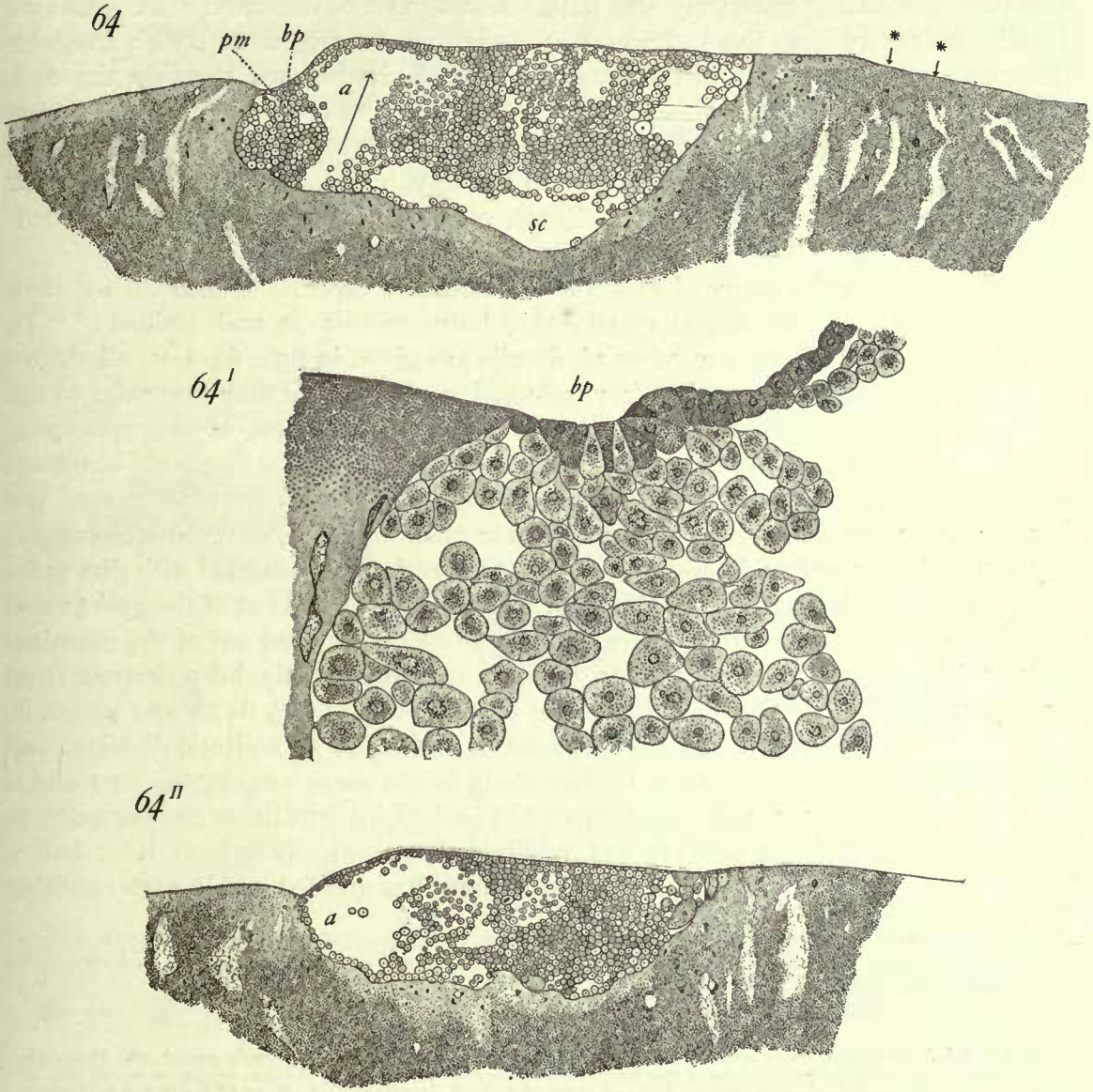


Fig. 64.—Sagittal section of gastrula slightly older than the preceding. × 35. *a*, Archenteron; *bp*, position of former blastopore; *pm*, Cells of posterior lip of blastopore; *sc*, Segmentation cavity.
Fig. 64[I].—Detail of preceding section showing the region of the blastopore.
Fig. 64[II].—Lateral section from the series from which fig. 64 was drawn.

become closed, owing probably to stress arising from the rapid extension backward of the entire blastoderm; and we note in this connection the greatly compressed character of the cells. Parenthetically, we may also call attention in another

section (fig. 64 A) to the great number of amitoses occurring throughout the germinal wall, and on the other hand, the absence of mitoses in this region. Referring again to fig. 64, we interpret the cavity *a* as the archenteron of the earlier stage which has deepened and reached the germinal wall, still preserving its smooth posterior boundary, but dilated anteriorly and fading into a mass of detached cells. And we identify the cavity *sc* as the segmentation cavity now enlarged and with irregular offshoots. Another section of the present specimen shows, near the side, fig. 64^{H}, the marginal extent of the dilated archenteron and the obliteration in this region of the segmentation cavity. Its major interest, however, is in contributing data concerning the relation of the blastoderm to the yolk. Especially at the anterior end we observe that the cellular elements, of great size, have recently become detached from the yolk.

The details in the study of this specimen deserve especial comment, for they indicate an intimate functional relationship between mitosis and amitosis.* To illustrate these conditions a number of details are given in figs. 64 A–N, all drawn from the foregoing specimen, but from selected sections. We may first refer to the character of the merocytes. In a detail of the anterior end of this specimen, fig. 64 A, over fifty merocytes are present, most occurring in the fine yolk, but some in a superficial rift of coarse yolk which spreads inward toward the blastoderm. We observe: numerous amitoses; the masses of fine yolk whose distinct outlines suggest polynuclear blastomeres; at one point (near 1) a nucleus surrounded with fine yolk, altogether suggesting a single blastomere; blastomeres formed out of the yolk (2 and 3); a large clear blastomere (4) which appears to have budded out of the germinal wall; and (5) a small clear blastomere, which has undoubtedly been derived from the adjacent yolk. At the opposite end of the blastoderm (fig. 64 B), and within it, is a large cell containing many nuclei, some of which are in amitotic division, and similar appearances are observed further along in the same section, fig. 64 I and J. In the first of these, I, a large blastomere has broken up into three smaller cells, in the largest of which the nucleus has subdivided amitotically into at least half a dozen smaller ones; in the second, J, a blastomere has divided and in each resulting

*The merocytes here considered are regarded as products of the segmentation nuclei. The difficulty, however, in distinguishing finally between the merocytes derived from the segmentation nuclei or from the sperm-heads has already been commented on (p. 57).

Figs. 64 A–N. Details of sections of preceding stage. (See page 67.)

A. Detail of germinal wall at extreme anterior end of blastoderm. 1–5, cells which are arising, or have recently arisen from the germinal wall. There can be little question from the yolk-filled character of some of these that they have recently arisen from the germinal wall (i. e., they can not be cells which are being passed into the germinal wall, as His suggests). Such a cell as that indicated at 5, although destitute of yolk material, is so far from the remaining cells of the blastoderm that it could only have been budded off from the germinal wall.

B. Detail of the posterior rim of blastoderm showing the origin of blastomeres from the yolk wall. Observe that some of the cells are filled with coarse yolk; others, 3, have relatively little. The cell, 2, just separated from the germinal wall, contains a number of (amitotic) nuclei.

C. Detail of wall of germinal yolk. 1, 2, 3, Nuclei arising amitotically, passing in the direction of the floor of the subgerminal cavity. 4, Blastomere arising from the germinal wall. 5, Blastomere undergoing amitosis. 6, Blastomere arising from the germinal wall, and showing aster.

D. Origin of blastomeres from the germinal wall. 4 and 5, Blastomeres recently separated. 1, 2, and 3, Nuclei about to be passed into blastomeres.

E. Yolk-filled cell arising from the germinal wall, and exhibiting typical mitosis. Adjacent is a blastomere whose nucleus is dividing amitotically.

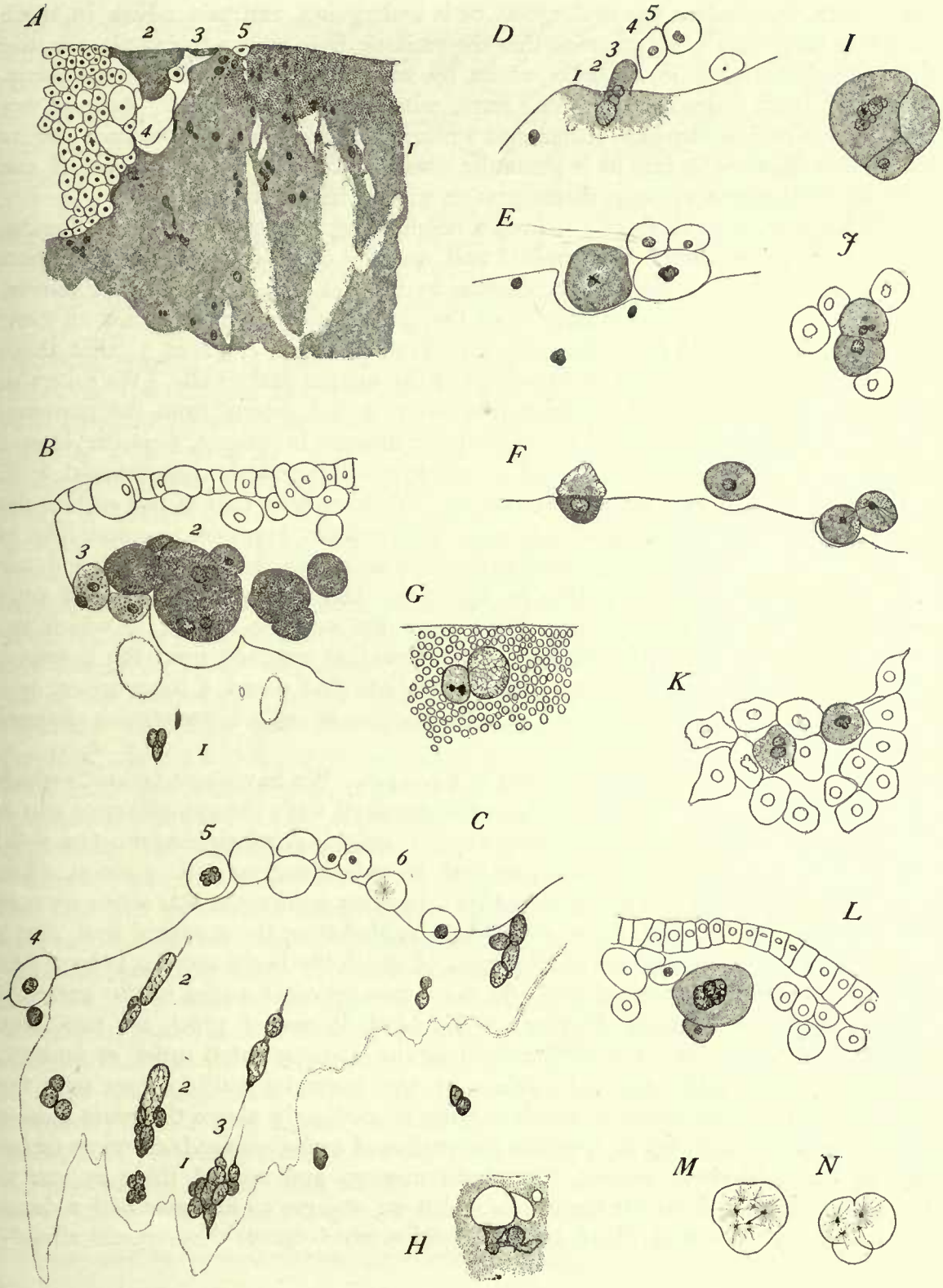
F. Blastomeres newly arisen from the germinal wall.

G. Vesicular nuclei in region near surface of germinal wall.

H. Vesicular nucleus, undergoing amitotic division, with adjacent vacuolar spaces.

I, *J*, *K*, and *L*. Cells of blastoderms in some of which amitosis is taking place.

M and *N*. Cells of blastoderm dividing by atypical multiple mitosis.



Figs. 64 A–N. Details of sections of preceding stage. (See bottom of opposite page.)

blastomere the nucleus has undergone, or is undergoing, amitosis. Now in these instances there can be no question that the amitotic divisions are taking place within the blastoderm itself, in a region where, by analogy, mitosis alone should occur, and where later, indeed, in the same form, mitoses alone are found. And we are thus constrained to conclude either that amitosis and mitosis are processes not as immutably different in fate as is generally assumed, or that at a later period the amitotic blastomeres undergo disintegration within the blastoderm.

But to continue: In fig. 64 C, from a neighboring section, we observe as before amitosis occurring within the germinal wall, and this type of nuclear multiplication appears active to an extraordinary degree, as the detail, 1, indicates. Moreover, with this activity, there is evidence from the greatly elongated character of some of the nuclei, 2, 2, and from the evident trails which occur, *e. g.*, at 3, that these nuclei are passing rapidly in the direction of the surface of the yolk. We note also that cellular increments, *e. g.*, in such a cell as 4, are arising from the germinal wall, and, as in the former specimen, amitotic division is present, 5, in the blastoderm proper. Adjacent to this, and in as close relation with the germinal wall, there is also evidence of mitotic division, 6. We have seen that in this section the cell 4 is arising out of the germinal wall; if any doubt exists as to possibility of cells to arise from the germinal wall at this late stage, we may refer to the detail shown from a neighboring section in fig. 64 D. Here is present a row of cells arising in this manner: in the wall itself occur the nuclei 2 and 3, of which the latter is passing into a lobe-shaped process budding outward from the germinal wall. From their position we may safely conclude that 4 and 5 have arisen in a similar way. We observe, finally, that the nucleus in cell 5 is undergoing changes in the direction of amitotic division.

Another interesting detail is given in fig. 64 E. We have here two cells which appear to have arisen side by side from the germinal wall; the cytoplasm of one is clearer, more differentiated apparently than its neighbor, which contains fine yolk, yet the nucleus of the cell lacking in yolk is undergoing amitotic division, while that of its neighbor is dividing mitotically. In other sections in this series we note the following details: Fig. 64 F, a cell half budded from the germinal wall, also a pair of cells evidently in stage of telophase, of which the lower appears to have just budded out from the germinal wall; fig. 64 G, two reticular nuclei in the germinal wall, products of amitotic division (*cf.* fig. 64 C), in one of which are two large chromatin masses; fig. 64 H, nucleus undergoing a complicated series of amitotic divisions; this occurs near the surface of the germinal wall, and we note the presence of vacuoles, three in number, lying immediately above the main masses of the dividing nuclei; fig. 64 I, within the outline of a single large blastomere occurring in the blastoderm proper, three cells appear, and two of these appear to have been derived from the largest, in which we observe as many as half a dozen nuclei; fig. 64 J, a cell in a late stage of division which shows three nuclei already

separate in one of its daughter cells, and the nucleus in the other about to undergo amitotic division; fig. 64 K, a nucleus similar to the last occurs in a cell high up in the blastoderm, and near it a cell which has undergone amitosis; fig. 64 M and N, two cells which are undergoing an extraordinary type of division; they contain many asters, conspicuous centrosomes, but no chromosomes; in N the cell is subdividing into three daughter cells.

The significance of these phenomena is commented upon on a later page, in the discussion of megaspheres and yolk nuclei in their relation to germ layers.

To resume the question of gastrulation:

The third stage in the writer's material is represented in surface view in plate V, fig. 31. It differs from the earlier stage shown in this way, plate V, fig. 30, in the following regards: (1) The circumgerminal ring, which had gradually been extending and carrying its nuclei peripherad, has faded out over the surface of the yolk, its proximal zone now alone noteworthy. (2) There is a conspicuous antero-posterior differentiation. The region of the blastopore is indicated by a short transverse shadow, marking the cavity of the archenteron, and the segmentation cavity is denoted by a broad transverse area, the ends of which as they approach the rim of the blastoderm bend backward, giving a somewhat crescentic shape. Three sections of this blastoderm are figured, the first, fig. 65, is sagittal, the second, fig. 65 A, passes between the points *A–A*, shown in the surface view, the third, fig. 65 B, between the points *B–B*. Comparing the sagittal section fig. 65, with that of the earlier stage, fig. 64, we observe increased growth at the posterior rim of the blastoderm; the germinal wall instead of shelving forward, now shelves backward, especially near the surface of the egg, still having below a sharp shoulder* against which lies the remains of the posterior lip of the blastopore, *pm*, of earlier stages,—this region, in short, is being overgrown by the blastoderm as it progresses hindward. The archenteron thus remains, as at *a*, separated only imperfectly from the segmentation cavity, *sc*, which is now of great size. This condition, indeed, is well shown in the more lateral sections, figs. 65 A and B, and they indicate as well the narrow limits of the archenteron; the sides of which, it will here be seen, are practically confluent with the sides of the segmentation cavity. As in the preceding stage, noteworthy relations exist between the blastoderm and the yolk. We observe, for example, that in the more lateral section a tongue of coarse yolk passes inward close to the surface of the germinal wall, and we obtain evidence that the row of neighboring cells has been formed by actual outbudding. In these cells amitosis occurs, as in the previous stage. These cells, it may be remarked, do not long remain in their subjacent position, for, identified by the coarse yolk they contain, they can be traced into the blastoderm and are found widely scattered among other cells.

* *Vis-à-vis* is a second shoulder which corresponds to the anterior germinal wall of the stage shown in fig. 63. In both regions, then, the blastoderm has overgrown the surface of the egg.

The fourth stage in gastrulation appears in surface view in plate v, fig. 32, and is but two days older than the preceding, plate v, fig. 31. It shows the following advances: (1) The embryo proper makes its appearance in a small depression, and is conspicuous on account of the dark adjacent shadows; (2) the center of the blastoderm rises as a circular plateau, leaving at its base a well-marked flattened rim; surrounding this the circumgerminal ring has largely faded away, its nuclei

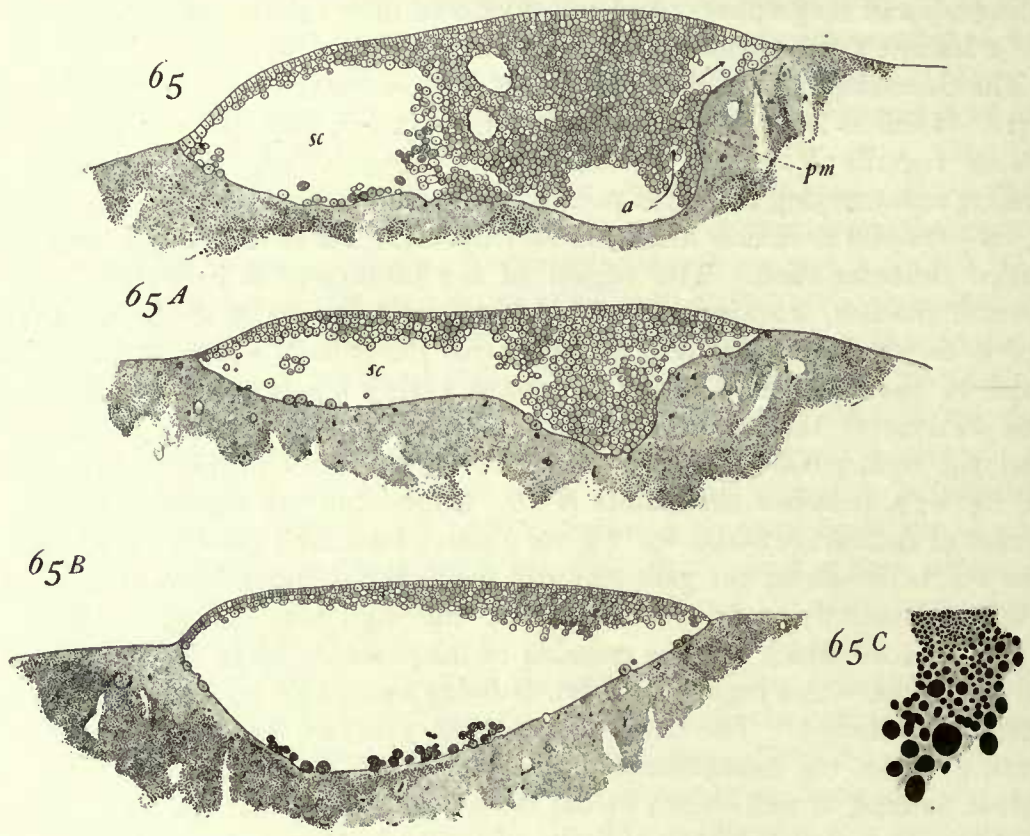


Fig. 65.—Sagittal section of gastrula slightly older than the preceding.
a, Archenteron. *sc*, Segmentation cavity.
pm, Posterior mass of cells (in region of ventral lip of blastopore).
Fig. 65 A.—Section parallel to preceding, but situated further at the side.
Fig. 65 B.—Section parallel to preceding, but more nearly marginal.
Fig. 65 C.—Detail showing coarse yolk.

now having passed far out over and into the yolk;* (3) anteriorly the segmentation cavity is becoming restricted to a small area, appearing in surface view as a light-colored tract near the rim of the blastoderm. Two sections of this blastoderm are figured, one sagittal (fig. 66), the other (fig. 66 A) passing between the points *A*–*A* shown in surface view. Contrasting the sagittal section (fig. 66) with that of the

* The figure represents the circumgerminal zone as too wide and conspicuous, an inaccuracy which was noticed too late for correction.

earlier stage (fig. 65), we notice that (*a*) almost the entire flattened rim of the blastoderm has been added; that (*b*) in the posterior portion of this rim the ectoderm is already differentiating the medullary plate of the embryo, *m*; that (*c*) the major growth has taken place backward—in witness of this, contrast the distance between the anterior end of the archenteron and the posterior rim of the blastopore in these two stages; that (*d*) in this connection the main cell-mass extends itself dorsalward and becomes the plateau-like region of the blastoderm; that (*e*) the germinal wall rising abruptly beside the archenteron in the earlier stage becomes excavated in

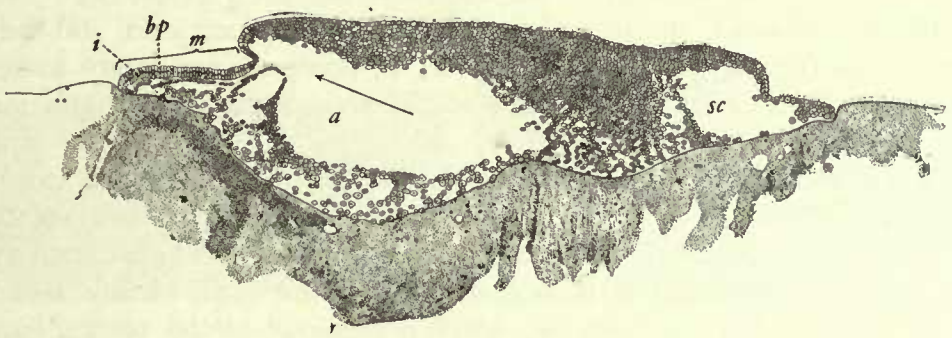


Fig. 66.—Sagittal section of gastrula in which the embryo is appearing.

a, Archenteron.
i, Region of outermost margin of ventral lip of blastopore.
pm, Posterior mass of cells (in position of ventral lip of blastopore).
bp, Region of blastopore.
m, Thickening in medullary plate of embryo.
sc, Segmentation cavity.

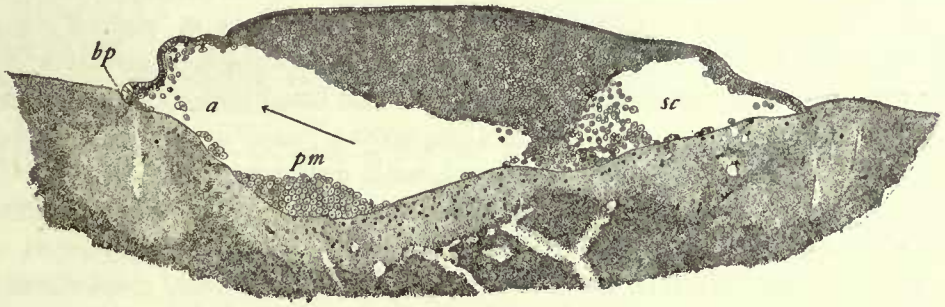


Fig. 66 A.—Section (lateral) parallel to the preceding.

the later, a portion of its material, at least, being represented by the spongy mass of cells which now forms the floor of the archenteron, *a*; that finally (*f*) there is evidence that the posterior rim of the blastoderm is rolling inward, the surface of the blastoderm growing more rapidly in this region than the lower layer with which it is connected. Detailed examination of the sections, however, leads us to the belief that the process of inrolling extends only as far as the point *i* (fig. 66); just above this the inrolled rim of the blastoderm merges with the cells arising from the germinal wall, and from this point inward openings occur between the cells and communicate with the archenteron. The section (fig. 66 A) already referred

to as passing slightly to one side of the sagittal plane shows favorably the thickening of the ectoderm at the side of the medullary plate and its inbending. We here observe also the reduced size of the segmentation cavity, the thickening of the cell mass roofing the archenteron, and the thinning out of the mass of cells, *pm*, forming its floor.

We may at this point consider conveniently the general bearing of the process of early gastrulation in the Chimæroid. We have seen that:

(*a*) In an early stage an archenteron was present (fig. 63), whose ventral wall was composed of cells and whose axis was at right angles to the surface of the blastoderm.

(*b*) In a second stage, the area of the blastoderm had increased, and the blastopore was closed (fig. 64); its position (fig. 64 A), however, accurately located, but more posterior than in the first stage; also the archenteron has greatly increased in size.

(*c*) At a third stage (fig. 65), the location of the blastopore can not be accurately determined, although it is certainly near the hindmost point of the blastoderm; the archenteron is less definite, and its long axis, which remains parallel to the neighboring germinal wall, becomes tilted backward, as indicated by the arrow in the figure: and the cells, *pm*, which correspond to the ventral (posterior) wall of the archenteron, now occupy a position further under and further forward than in earlier stages, in consequence of the hindward extension of the blastoderm.

(*d*) Finally (fig. 66), this hindward extension is so expressed that the position of the early blastopore shifts under the rim of the blastoderm and comes to appear at the point *bp;* concomitantly the archenteron increases in size, its axis lying nearly parallel to the surface and its ventral wall developing extensively both in thickness and in (anterior) extension. From these conditions it follows that in the later gastrulation of Chimæra we are dealing with a reopening of the blastopore of an earlier stage. Accordingly, in contrast with gastrulation in sharks, Chimæra preserves the primitive blastopore within the blastoderm itself. This stage, however, is an evanescent one. In connection probably with a change in nutritive values, whereby the yolk is passed to the archenteron from a source more and more postero-ventral there is a constant tendency for the cells of the archenteron to be drawn, both in ontogeny and in phylogeny, closer to the source of nutriment. For this reason the cells of the archenteron multiply more rapidly from below than from above (*i. e.*, the region where primitively they were invaginated from the ectoderm) with a result that the blastopore becomes of less and less importance in early stages. It is suggested, also, that during this growth there is a constant convection of the cells of the blastoderm, in the process of which elements formed in the region of the posterior wall of the archenteron pass downward and forward. *Pari passu*, the posterior rim of the blastoderm, including the region of the blastopore, extends first backward, then downward and inward; it thus comes finally to lie under the rim (*i. e.*, the later rim) of the blastoderm.

We have emphasized these conditions of growth in Chimæra, since they serve, I conclude, to explain the gastrulation of the shark, a process so puzzling that Samassa (1895) has even gone so far as to deny its presence, *sensu stricto*, in this group. According to the present interpretation the primitive shark had, like Chimæra, a blastopore which opened *near* but not at the rim of the blastoderm; in this position it next became a rudimentary organ, since, apparently, the conditions governing the increase of cells in the archenteron suffered a change—inasmuch as they came to receive their nutriment directly from the neighboring germinal wall instead of indirectly, *i. e.*, through a process of continued invagination at the blastopore. Accordingly, in the development of modern sharks the blastopore

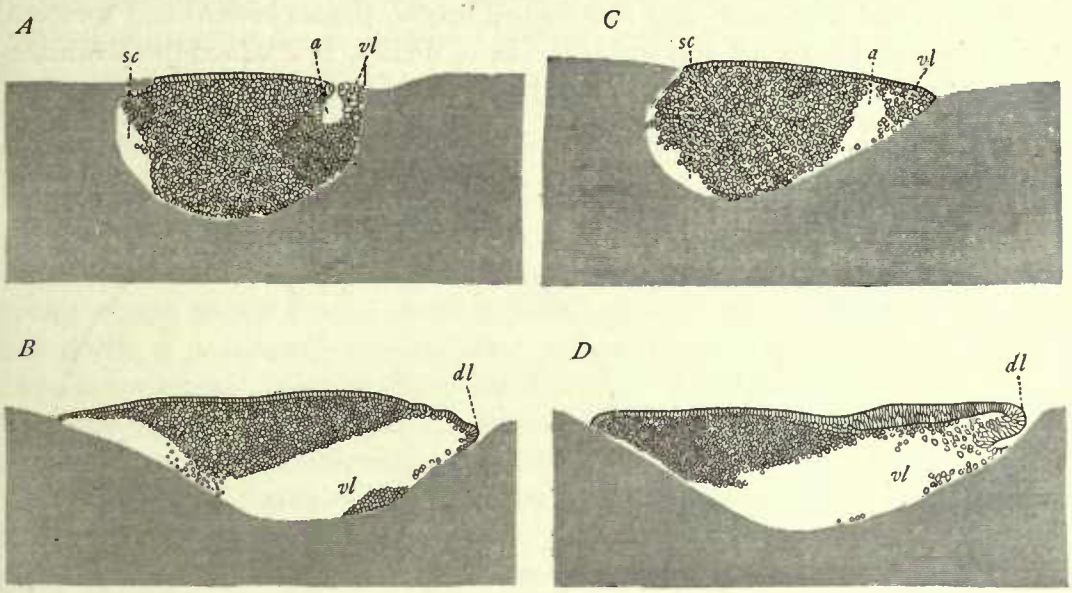


Fig. 67.—Diagrams comparing gastrulæ of Chimæra and Selachian. *A* and *B*, Earlier and later stages in gastrula of Chimæra colliei. *C* and *D*, Earlier and later gastrulæ of shark (mainly after Rückert).
a, Archenteron. *dl*, Dorsal lip of blastopore. *sc*, Segmentation cavity. *vl*, Ventral lip of blastopore.

fails to appear within the blastodermal disc, since here it has long been functionless. But obviously the blastopore would again become important in the economy of gastrulation, if nutritive material were brought into its neighborhood by any process in the growth of the blastoderm or in the encroachment of the germinal wall. Thus we may infer that it would again become a functional organ when its position was transferred to the rim of the blastoderm. In this position it still occurs exceptionally, as C. K. Hoffman has shown in Acanthias,* or it may indeed reopen deeper under the rim of the blastoderm, as the majority of investigators maintain.

* In a letter, which I am permitted to quote (July, 1903), from Professor Hoffman, the comparison is accepted as follows: "In Chimæra the blastopore is located *near* and in Acanthias *at* the rim of the early blastoderm. For the rest the archenteron and the open blastopore of Acanthias agree entirely with those of Chimæra. Acanthias forms the bridge (in this regard) between Chimæra and other sharks and furnishes us the key to the problem of gastrulation of the other sharks."

To make the comparison of the gastrulæ of Chimæra and Shark more concrete we have figured two stages side by side (fig. 67, A and C, B and D). We need only add to the foregoing text the remark that the archenteron and segmentation cavity are more distinct in Chimæra, and that the differentiation of the embryo takes place in a more restricted area. We append also (fig. 68, A, B, C) a scheme expressing our interpretation of the mode of origin of the meroblastic gastrula in this form. In A is pictured a sagittal section of an early gastrula of a holoblastic type, and between the points marked with asterisks is indicated the narrow zone below which the amount of yolk is supposed to have notably increased. In B, the second stage in this evolution, is a condition not unlike the late gastrula in Chimæra: The yolk mass still segments, and the ventral lip, *vl*, passes inward and forward as the dorsal lip rolls backward and inward. In C, finally, is attained the condition in sharks: Archenteron and segmentation cavity merge; segmentation is lost in the

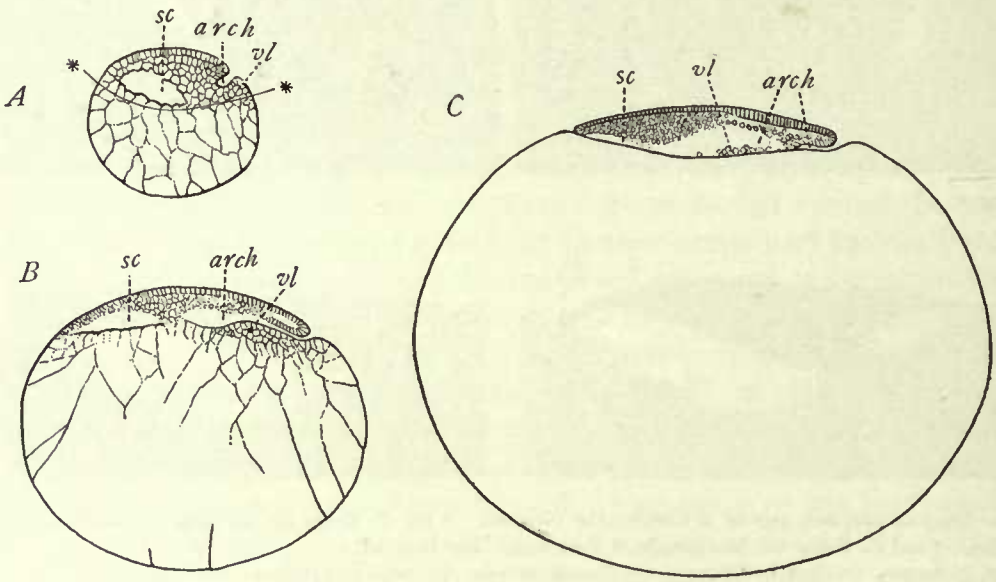


Fig. 68.—Diagrams suggesting origin of meroblastic character of egg of shark.

A. Sagittal section of early gastrula of holoblastic egg (e. g., Petromyzon). *B*. Section showing conditions similar to those in Chimæra colliei (cf. fig. 66). *C*. Section of gastrula of shark. *arch*, Archenteron; *vl*, ventral lip of blastopore; *sc*, segmentation cavity.

yolk mass, and the latter comes to pass its nutriment into the blastoderm indirectly, *i. e.*, as nourishment for the growth and multiplication of the cells already formed, instead of directly, *i. e.*, in the form of new yolk-filled blastomeres, and from this process there results a smooth germinal wall. This interpretation agrees in general with that lately restated by Ziegler (Lehrbuch Entwicklungsgeschichte, 1901, pp. 352–353); it differs in the interpretation of the fate of the ventral lip of the blastopore. According to the older view the ventral lip remains more or less passive, in the present interpretation it has undergone a marked change; the cells which primitively formed the ventral lip of the blastopore are to be sought in the region *vl*, on the floor of the archenteron. The *de facto* ventral lip of the blastopore (*i. e.*, in all stages but the earliest) is accordingly a secondary structure, which arises from the new conditions attending the overgrowth of the blastoderm.

LATER GASTRULÆ.

Surface views of three later gastrulæ are pictured in plate v, figs. 33–35, a series in which the body of the embryo becomes distinctly differentiated. In the first it occurs as a lip-like thickening, the blastoderm itself having become somewhat larger in diameter and flatter than in the previous stage. In the present specimen, which was examined after my interest was aroused in the matter of the peripherad migration of the yolk-nuclei, these structures could be seen* spread out widely over the neighboring surface of the yolk. The second stage, plate v, fig. 34, resembles outwardly a shark embryo at Balfour's stage B; the light area in the anterior and median portion of the blastoderm, which marks the cleavage cavity, is, however, larger than in any selachian hitherto described. In the third stage, plate v, fig. 35, the embryo arises as a knob-like eminence, its tail end projecting somewhat over the edge of the blastoderm; anteriorly the surface of the blastoderm becomes thin and transparent, and it here assumes a peculiar vesicular character.

Details of the Later Gastrula of Plate V, Fig. 35.

This stage, although scarcely later than Balfour's stage B in shark nomenclature, is remarkable for the concentration of its elements. Thus, if we compare it in point of size with a similar stage in Pristiurus, measuring it always in terms of its blastoderm, it is of much smaller size. At this stage the length of an embryo of Torpedo measures about one-third the diameter of its blastoderm, that of Pristiurus about one-eighth, and that of Chimæra not more than one-twelfth. Moreover, its component parts are already more highly differentiated.

A number of details of this stage are given in plate vi, fig. 39, and figs. 39 A–E. In the first of these (fig. 39) the embryo with its adjacent blastoderm is viewed as an opaque object; it appears next in similar position (A) but as a transparent object, showing ectoderm, entoderm, and archenteron. Behind the embryo the surface of the yolk shows a series of lines representing either surface fissures or vacuoles, related, as we have concluded, to lines of cleavage. In the following figures the embryo is viewed from an antero-dorsal direction (B), postero-dorsal (C), postero-median (D), and postero-ventral (E). The mesoblast is well indicated in plate vi, fig. 39 B, also the extent of the thickening of the ectoblast forming the posterior margin of the embryonic body. In connection with these figures we may refer to the series, fig. 69 A–M, drawn from sections of this embryo cut parallel to the neighboring rim of the blastoderm (*i. e.*, transverse, although slightly oblique to the axis of the embryo), and point out the following features: (1) The size and definiteness of the gut, an important factor in establishing the contour of the embryonic body; the gut acquires the cavity, *gc* (which communicates with the yolk region only for a short space near the rim of the blastoderm, *c*, and accumulates around its anterior end the bulk of the mesoblast, *mes*). (2) The fusion of ecto- and entoblast occurring not merely *at* the tail end of the embryonic body but

*The circumgerminal zone is, however, shown too distinctly in the present figure; its color should resemble rather that in plate v, fig. 34.

far forward, almost to the end of the embryonic gut, the band of fusion extending in a narrow zone as denoted at *x*, fig. 69 II. (3) The concentration of the yolk-entoblast under the embryonic body; this becomes conspicuous quite in front of the embryonic gut, then merges with the gut, then separates from it, and, as the lumen of the gut opens out ventrally, it proceeds backward in a layer finally rounding

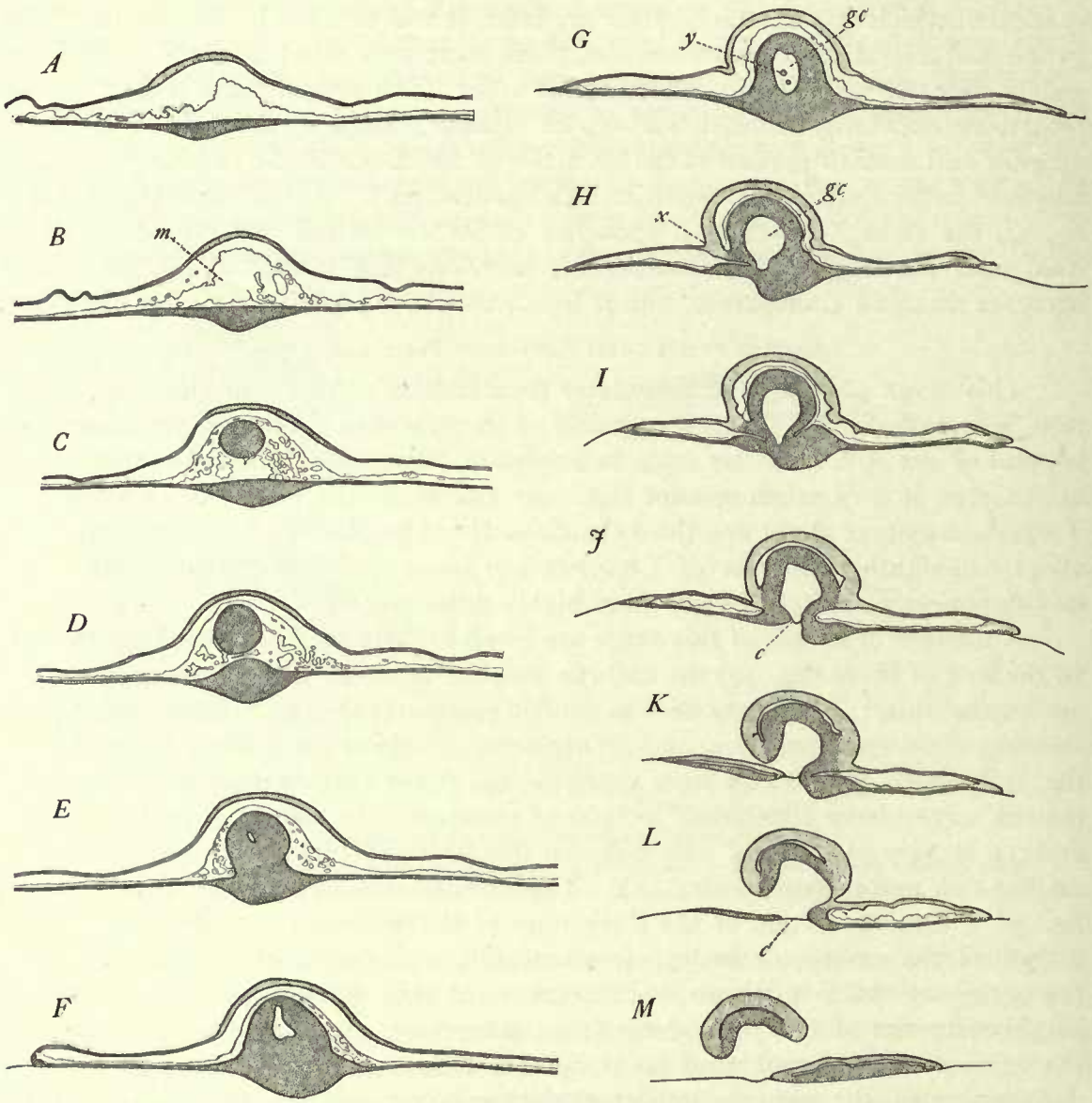
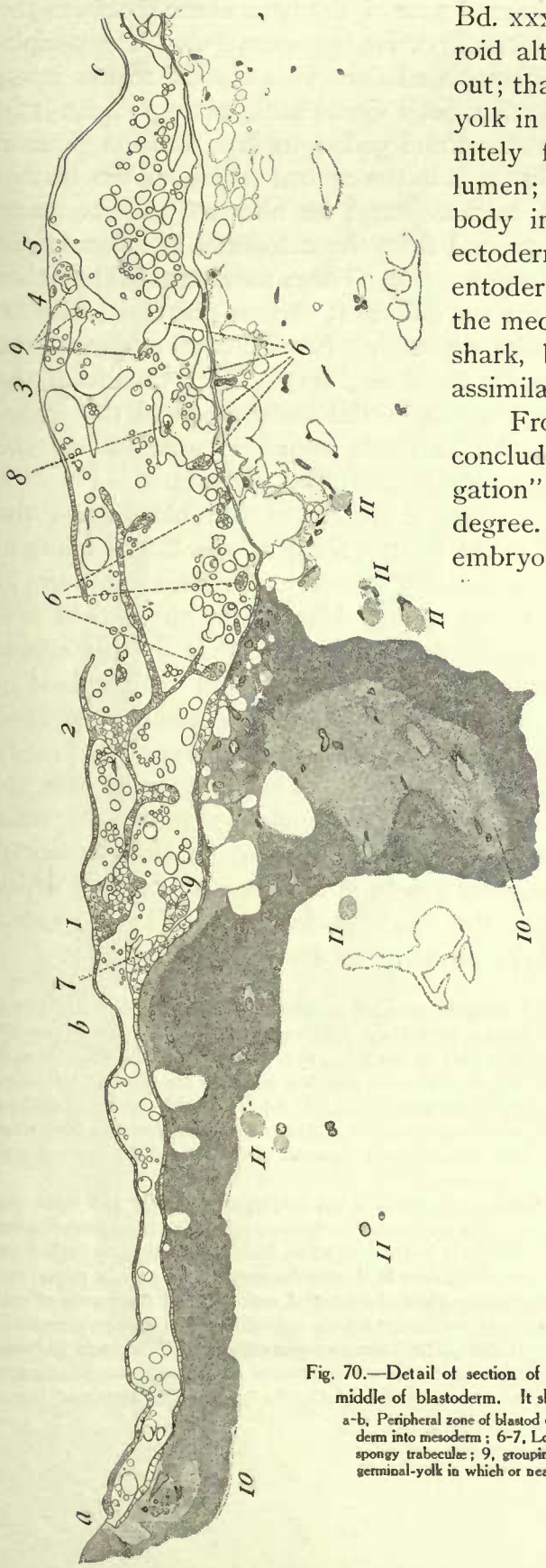


Fig. 69 A–M.—Transverse sections through early embryo and neighboring blastoderm of stage corresponding to that of plate V, fig. 35. The series passes from in front backward.

c, Yolk region intruding between caudal folds; *gc*, gut cavity; *m*, mesoblast; *y*, yolk lying in cavity of gut; *x*, fold near posterior end of embryo where ectoderm and entoderm merge.

outward on either side. (4) The presence in the cavity of the embryonic gut of small masses of the disintegrating segments of the egg (fig. 69 G, *gc*), which serve probably as food, interesting in connection with the fate of the yolk in Chimæra (*cf.* in stages of Plate VIII). Contrasting the foregoing conditions with those in an elasmobranch in stage B (*e. g.*, as shown by the Zieglers, Archiv f. mikr. Anatomie,



Bd. XXXIX, Taf. III), we note that the Chimæroid although smaller is much less flattened out; that the gut which is flattened against the yolk in the elasmobranch is in Chimæra definitely formed and provided with a distinct lumen; that the lateral contour of the embryo's body in Chimæra is already developed, the ectoderm in the hinder region fusing with the entoderm; that the yolk entoblast thickens in the median axial line, a feature lacking in the shark, but important doubtless in the early assimilation of the yolk.

From the foregoing details one is led to conclude that in Chimæra "precocious segregation" has been developed to a noteworthy degree. In spite of the small size of the embryo, both relatively and actually, it has already made strides in the direction of attaining its definite form, outstripping in these regards the elasmobranch; thus it has already developed gut outline, definitely arranged the mesoblast, separated practically the sides of the embryo from the blastoderm, and has specially concentrated the yolk entoblast in the axial region. Accordingly, in these regards, Chimæra stands separate from the elasmobranchs; transitional, however, is Callorhynchus, judging from figures recently given by Schauinsland (*e. g.*, in his plate XII).

An idea of the complicated nature of the blastoderm at this stage (plate V, fig. 35), both in itself and in its relation to the yolk, may be had by examination of fig. 70. This represents part of a section which passes through the blastoderm transversely, somewhat in front of the embryo.

Fig. 70.—Detail of section of preceding embryo. The section is transverse and passes near middle of blastoderm. It shows particularly the early differentiation of the vacuolar area.

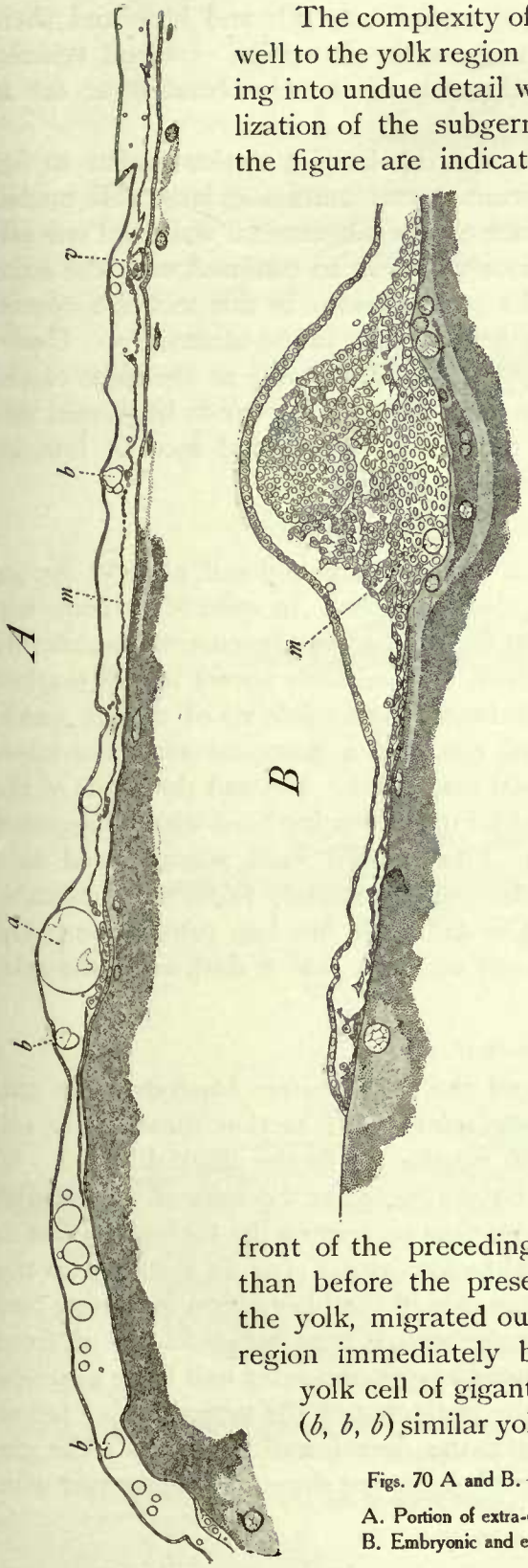
a-b, Peripheral zone of blastod erm; b-c, central region of blastoderm; 1-5, centers of proliferation of ectoderm into mesoderm; 6-7, Lower ends of these proliferations in their relation to entoderm; 8, amitosis in spongy trabeculæ; 9, grouping of mesoderm cells to form vessels; 10-11, centers, large and small, of germinal-yolk in which or near which nuclear elements are dividing amitotically.

We notice, first of all, that the peripheral zone of the blastoderm (between the points *a–b*) is less complicated than its central portion (between *b–c*). The peripheral zone is, however, more highly differentiated than in a similar region in an elasmobranch (*cf.* Rückert's memoir in Kupffer's Festschrift, plate VII, fig. 75); witness the definite character of the ectoblast and yolk entoblast, and the gigantic size of many of the mesoblast cells. But it is in the central region of the blastoderm where the conditions are most extraordinary; we observe, that at many points, 1–5, masses of cells extend downward from the ectoderm, proliferating in ridges, sometimes giving rise to root-like processes. These terminate below either freely, or they may actually fuse with the entoblast; at various points, 6, they lie close to the entoblast; at 7 is shown a point where they become continuous with the entoblast (the continuity to be traced in the serial sections). They thus form the spongy meshwork which we have already noted in the surface view of this stage, a condition of complication, which, as far as I am aware, is unknown in the extra-embryonal blastoderm of so early a stage in any other vertebrate.

We note in connection with the spongy character of the blastoderm the presence of many large cells (unshaded in the figure), some of which, like many in the neighboring spongy trabeculæ, are undergoing numerous divisions (amitotic) as at 8.* To understand the meaning of this spongy blastoderm one should first consider it in its prospective value. Later specimens show that in this region appear blood-vessels, and in the present early preparation—and even indeed in earlier ones, we are evidently dealing with the beginnings of vascular structures. In fact in the trabeculæ themselves we find at various points (9) the cells already grouped together so as to form cavities, and in the latter large granular cells are undergoing subdivision, in the direction evidently of blood-building. In this character again, it will be remarked there is given an important instance of the precocious mode of development of Chimæra. In other words, in this form at a period which outwardly suggests stage B of the shark the vascular development in the extra-embryonal blastoderm is (approximately) equivalent to the shark's in stage E.

*We have here again evidence against the commonly accepted view (of Flemming, Ziegler, and von Rath) as to the significance of amitosis. Admitting that these cells come to form blood and blood-vessels, it must also be granted, as the following evidence shows, that the blastoderm becomes part of the young fish, and therefore the behavior of its cellular components is not to be compared with that of the vitellophagous periblast nuclei in the teleost. Of course it will be seen, on the other hand, that the adherent of the Flemmingian view might object that although the blastoderm itself was a permanent structure of the embryo it might none the less contain provisional cellular elements (nutritive). He will admit, however, that this rarified view as to the fate of component elements of the blastoderm receives little support from the examination of related elasmobranchian structures.

The present evidence, it seems to me, favors the view that amitosis is but a symptom of early and rapid cell-multiplication. Such a need for rapid division often occurs in evanescent structures, and hence it may happen that this type of division has been given less consideration than it is justly entitled to, from the standpoints both of cell physiology and cell philosophy. In this matter I need merely mention, in view of the scope of the present paper, that there is rapidly accumulating a mass of evidence against the decadent character of amitosis. In the nature of such evidence are the observations of Conklin (Am. Nat., Oct., 1903) on the egg follicle cells of Gryllus; Kellogg's results on similar structures in Hydrophilus (Science, Mar. 4, 1904); also H. L. Osborn's observations on Fasciolaria (Science, Feb. 5, 1904) in which amitosis occurs in stages of gastrulation; Boeke's statements that in teleosts mitotic may arise from amitotic nuclei (Petrus Camper, vol. II, Afl. 2, pp. 161, 1902); finally, Child's "Amitosis in Moniezia" (Anat. Anz., vol. XXV, 1904).



The complexity of the foregoing conditions (fig. 70) applies as well to the yolk region as to the blastoderm itself. Without entering into undue detail we may note the following: Extreme vacuolization of the subgerminal region (the vacuoles at the right in the figure are indicated by dotted lines); they usually occur in or in association with the lighter areas of the germinal yolk. If we regard the vacuoles in the earlier stage as retaining the character of intercellular spaces, they have by this time undergone, in part at least, change of function, serving now as nutriment purveyors to the yolk entoblast. In this connection we find that at various points, 10, the coarse yolk is traversed by fine yolk in rifts, whose shape suggests that of the vacuoles of earlier stages. In this fine yolk, moreover, many nuclei are present, and, judging from numerous amitoses, dividing rapidly. In addition to these rifts of fine yolk, we note that there occur at many places throughout the coarse yolk small areas of fine yolk, 11; these have in nearly every case nuclei in or near them, and we have thus ground for regarding the yolk region of the egg not as a syncytium *pur*, but rather as a mass of yolk-filled cells whose boundaries have broken down, but whose individuality as cells has not yet been wholly lost.

A second section of the extra-embryonic blastoderm of this stage is shown in fig. 70 A, a detail of a section passing through the blastoderm considerably in front of the preceding section. Here is indicated even better than before the presence of giant cells which have arisen from the yolk, migrated outward, and are undergoing division in the region immediately below the ectoderm. At one point (*a*) a yolk cell of gigantic size is shown (unshaded); at other points (*b*, *b*, *b*) similar yolk cells are undergoing division by amitosis.

Figs. 70 A and B.—Sections of stage of early embryo figured in fig. 69.

A. Portion of extra-embryonic region in section corresponding to fig. 69 B.
B. Embryonic and extra-embryonic regions in section similar to fig. 69 C.

Into this region extends a delicate layer of mesoblast (*m*); and here and there groupings of cells of this layer, as at *v*, suggest the formation of blood vessels. Under the gigantic cell, one notes that the cells of the mesoblast layer are of remarkable size.

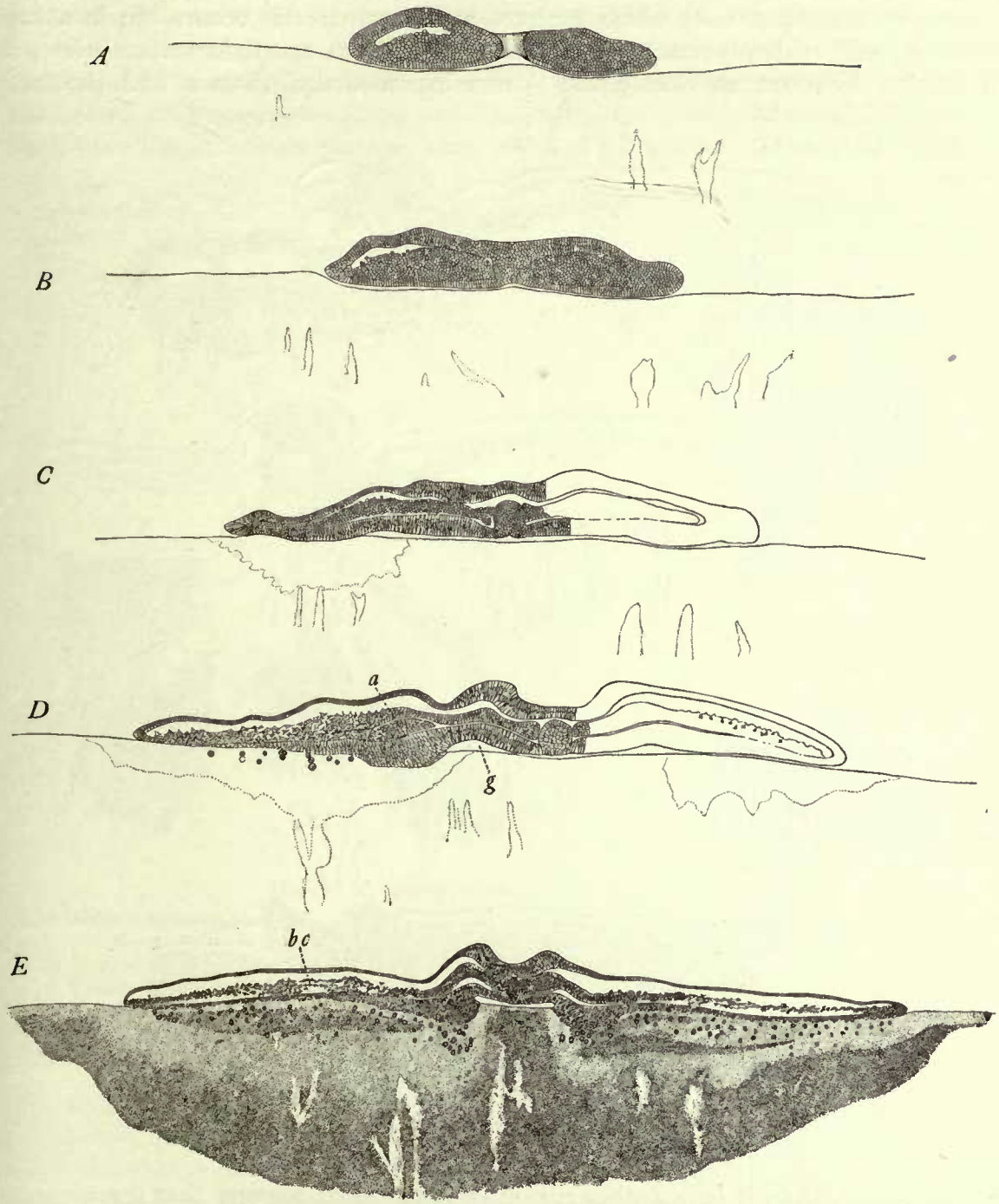
Another section, given in fig. 70 B, pictures details of a section similar to fig. 69 G. This illustrates particularly a subgerminal zone containing large yolk nuclei; of these some are situated close to the surface of the subgerminal wall, and one (*m*) has passed into the entoderm. This obviously cannot be confused with the adjacent entoderm cells, if only on account of its greater size. In this section a special area of formative yolk is shown underlying the periphery of the blastoderm. Under the embryo itself the formative yolk attains the surface notably at the sides of the embryonic body, and it is from this region that the cells appear to be passed into the embryo. Less activity is probably present in the ventral median line, on account of the quantity of coarse yolk which is here present.

Later Gastrula. Embryo With Open Medullary Folds.

This stage, figured in surface view, plate V, fig. 36, and in detail, plate VI, fig. 40, may be compared with Balfour's stage D in elasmobranch. In spite of the conspicuous growth of the embryo, the blastoderm, it may be noted, remains remarkably small in size. In this stage the blastoderm of Chimæra shows a well-marked central area, which on closer examination is found to be made up of spongy meshwork; there is also a somewhat thickened rim, and a marginal zone, the latter shown in sections to be formed of peristomial mesoblast. Beyond the limits of the blastoderm the surface of the yolk showed faintly diverging lines which suggested cleavage planes. (*Cf.* plate VI, fig. 39 A.) The embryo itself, when viewed as a transparent object, plate VI, fig. 40, shows shark-like medullary folds, more delicate, however, and narrower in proportions. The tail folds are less conspicuous; the mesoblast concentrating in this region shows on each side a dark area, the relations of which are referred to later.

Details of Stage D.

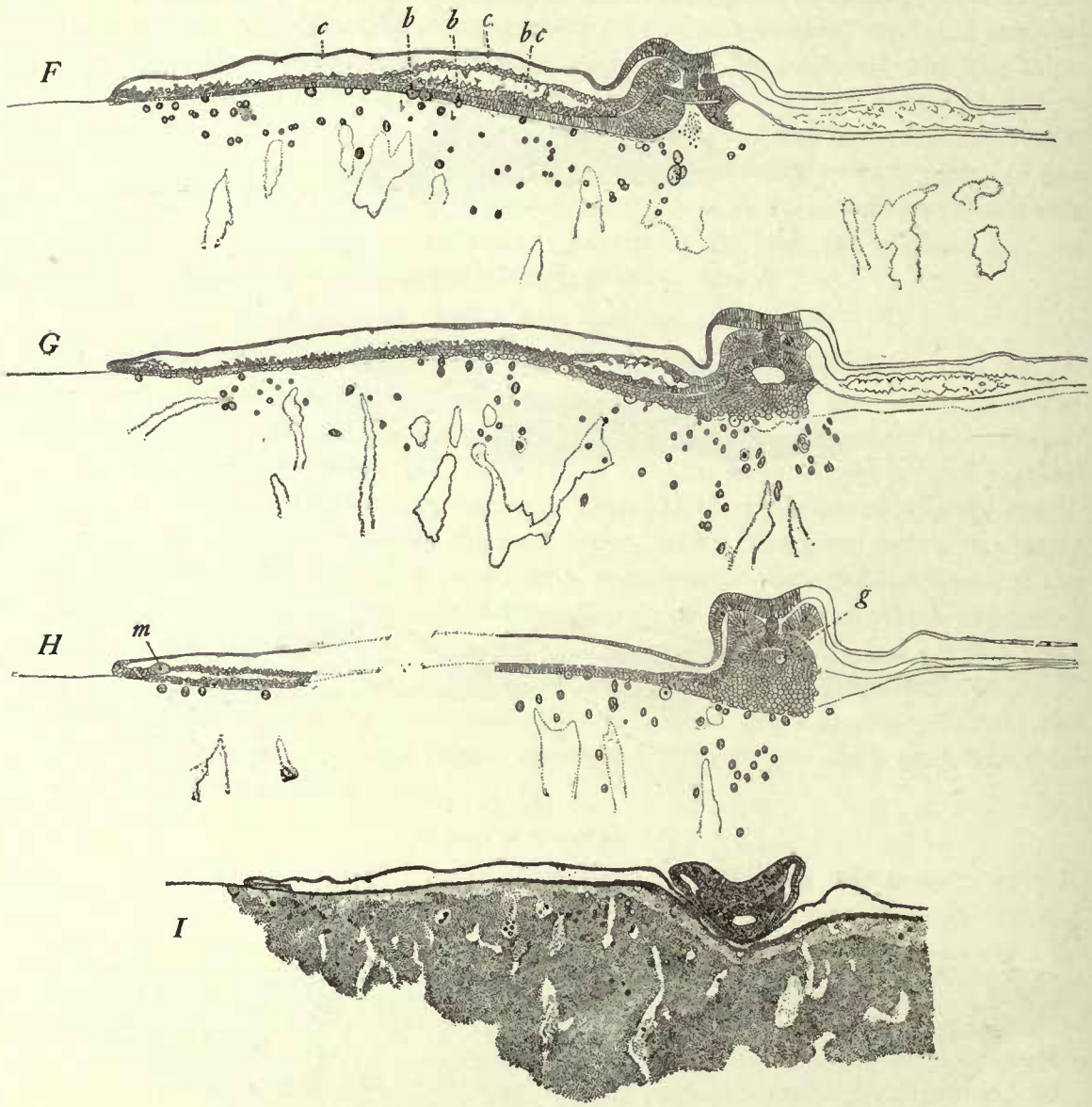
Transverse sections of the embryo and the neighboring blastoderm in this stage are pictured in fig. 71, A–I. Thus beginning with a section through the tail folds, we see in B, ectoderm and entoderm continuous in the chordal region. In this section the mesoderm merges with the entoderm not at the sides of the chordal region, but near the margin of the blastoderm, thus suggesting the theoretical condition in the origin of the mesoblast advocated by Graham Kerr. In section C (at the left side, the plane being slightly oblique) the side of the blastoderm is coming into functional connection with the yolk; the notochord is here being folded off from the entoderm; the latter is now a thick, flattened layer, its outer half lying apposed to the yolk wall. In D the section shows the beginning of the neural folds; below them is a well formed layer of mesoblast, also the dorsal wall of the gut; the gut lumen appears at *g*; at its side the dorsal wall of the gut shows a wide contact with



Figs. 71 A–E and continued F–I on page 82.—Transverse sections of late gastrula shown in Plate V, fig. 36. The sections pass forward; the first of the series, A, traverses the tail folds; the last, I, the head region of the early embryo.

a, Tongue of mesoblast cells representing the urogenital anlage; *b*, megaspheres in process of passing through the yolk-entoblast; *bc*, body cavity; *c*, points in extra-embryonic region where the ectoderm cells are being proliferated into the blastoderm; *g*, gut cavity; *m*, megasphere appearing in peristomial mesoblast.

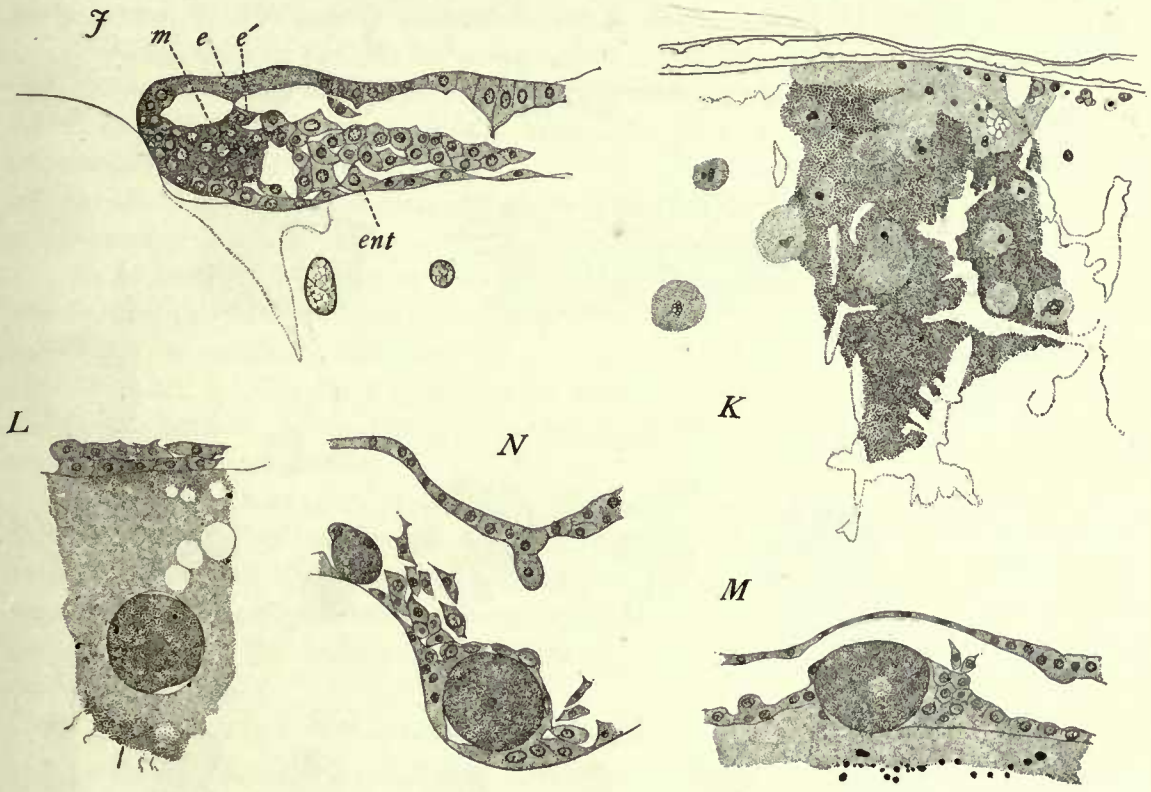
the yolk, and here at various points yolk nuclei are clustered, having evidently an important physiological relation with the overlying blastoderm; we note at *a* a tongue of mesoblast cells which projects medianward; this occurs but in a few sections, and evidently corresponds to the dark area noted in surface view; it resembles, however, so closely the "lame intermédiaire" (Swaen and Brachet)



Figs. 71 F–I. (For description and lettering see page 81, A–E.)

in the teleost, that, if for no other reason, we are led to suggest that it represents the precocious beginnings of the excretory system. In E the notochord has separated from the yolk, the gut lumen becomes narrowed, and lateralward the first trace of a body cavity (*bc*) appears. We observe that the margin of the gut passes directly into yolk-entoderm, the distinctness of its lower boundary having

faded away, and, *pari passu*, the yolk nuclei have greatly increased in number. In the region where the yolk-entoderm approaches the lumen of the gut it thickens and sinks downward, leaving as the floor of the gut cavity a wedge-shaped mass of germinal yolk. At the outer rim of the yolk-entoderm we observe that it becomes continuous with the mesoblast; in other words, recalling sections D and G, the peristomial mesoblast of Chimæra which now arises is *not continuous* with the gastral mesoblast. We have thus a reason for inquiring whether gastral and peristomial mesoblast



Figs. 71 J–N.—Details in sections of foregoing embryo (figs. 71 A–I).

J. Region of peristomial mesoblast.
e, ectoderm; *e'*, cells recently derived from *e*; *ent*, entoderm; *m*, peristomial mesoblast.

K. Detail of subgerminal yolk region showing cellular arrangement of merocyte elements.

L. Lying in the subgerminal yolk is a megasphere, which, on the evidence of the overlying vacuoles, is in the process of rising towards the yolk entoderm.

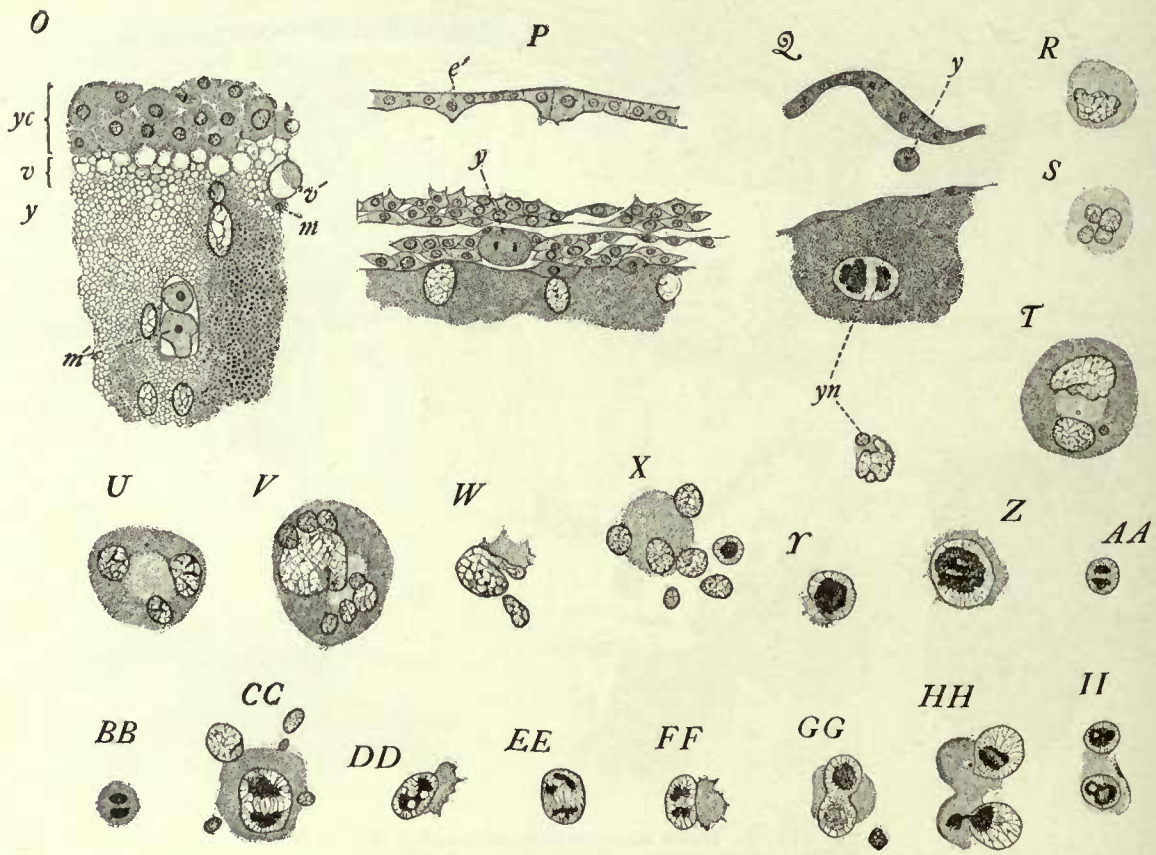
M. Similar megasphere passing into the yolk entoderm.

N. Megaspheres similar to preceding, but representing a somewhat later stage of passage into the blastoderm.

are as intimately related as we have generally assumed.* A condition of the peristomial mesoblast is figured in detail in J, and it proves of considerable interest, since the region of mesoblast proliferation is of wide extent. Not only are cells budded out from the marginal mass *m*, but we observe also that cells are added to the mesoblast from the neighboring ectoderm; thus at *e'* is a cell which has been derived from the ectoderm *e*, where, by the way, a syncytium is now present; and

Cf. the current view as to the secondary confluence of blastopore and yolk "blastopore," as summarized in Ziegler's *Handbuch der Embryologie*, pp. 352 and 353.

at the point *e* a mitosis is taking place preliminary to budding off another mesoblast cell. We conclude that the cell *e'* has been derived from the layer *e*, and not from the cell mass *m*, when we consider (1) that its granular contents agree in character with the layer *e* rather than with the mass *m*; (2) that a continuous boundary line separates the mass *m* from *e'*; and finally (3) that the cell *e'* is connected with the layer by a protoplasmic process, above which a nucleus in mitosis is present. Less evident, from this section at least, is the question whether cells are added to the



Figs. 71 O-II.—Details in sections of foregoing embryo (continued from page 83).

O. Detail showing transition between yolk region and the cells of the blastoderm.
m. Yolk nucleus lying against the wall of the vacuole *v'*.
m'. Yolk nucleus now lying within a vacuole, and transformed into a yolk-surrounded blastomere.
v. Zone of large vacuoles.
y. Zone of small vacuoles and fine germinal yolk.
yc. Yolk entoderm.

P. Detail of blastoderm, showing at *y* the division by mitosis of a megasphere lying in the yolk entoderm.

Q. Detail of section near the marginal region of the blastoderm, showing single megasphere, *y*, lying free in the space between ectoderm and yolk entoderm.
yn. Yolk nuclei undergoing division by atypical mitosis and by amitosis.

R–II. Details showing various phases of division in yolk nuclei.

peristomial mesoblast from the entoderm more proximal in position. At some points one is inclined to admit that such a cell as shown in J, *ent*, is being budded off into the tongue of mesoblast. (*Cf.* the condition shown in the section N.)

In the section F, the notochord is again continuous with the entoderm; the gut region rises, and its lumen is now walled with cells save in its median-ventral line. Here a thin wedge of yolk intrudes. Especially noteworthy is the relation of the yolk to the yolk-entoderm in this region. The latter has again a more

distinct ventral line of boundary, broken only at points, as at *b* and *b*, where cells from the yolk are entering. There can be no question in this regard since the entering cells are distinguishable as large in size, circular in outline, and granular in content. (*Cf.* sections L, M.) Another noteworthy feature in this section is that some of the ectoderm cells as at *c* and *c*, give off amœboid processes and, I am led to believe, later become detached, contributing to the growth of the mesoblast. A detail of this condition is shown in section J. We may finally note that the body cavity, *bc*, reaches its maximum size in this region of the embryo.

In G the floor of the gut becomes cellular; the notochord is again separate from the gut wall; and as before merocytes contribute directly to the growth of the yolk entoderm. In H the last-mentioned character is seen even to better advantage, for not only are the large yolk-cells passed into the lateral yolk entoderm, but they appear also high up in the central gut wall, as at *g*, and in the region of the peristomial mesoblast, as at *m*.

In I, finally, a section is shown passing through the region of the head tip, which now projects forward above the blastoderm. On either side of the gut the mesoblast is distinct, differing in this regard from the condition shown in an elasmobranch (*cf.* Ziegler's figure 19, II, Arch. f. mikr. Anat., Bd. XXXIX, Taf. IV). In the neighboring blastoderm, as in the shark, the mesoblast is limited to a small tongue of peristomial cells.

Before concluding an account of this stage two of its features still deserve comment. (1) The fissuring of the yolk region. The fissures are usually vertical, as indicated in all the foregoing sections, and may, as we have already seen, be regarded as homologous with cleavage spaces. (2) The mode by which merocytes become cells of the embryo. This heading, however, deserves to be treated in a more formal way.

The Transformation of Merocytes into Cells of the Blastoderm.

In this connection a number of details of sections of stage D have been figured, figs. 71 K–II, and in examining the series we find evidence, first of all, that merocytes move from a lower into a higher zone of the yolk. Thus, in fig. 71 O, the merocytes are elongated in the direction of the yolk-entoderm.* Also in the three sections L, M, and N we observe a great yolk cell (megasphere)† first deep in

*That this is connected with a migration of these elements in the direction of the surface of the cell mass is known by analogy—witness the behavior of slime cells in the skin of amphibians and fishes (*e. g.*, Homea).

†The megaspheres can have little to do with primitive ova, since they occur widely scattered throughout the blastoderm. Thus in fig. 71 H one is arising at the extreme rim of the blastoderm, in F several are seen midway between the embryo and the rim of the blastoderm, in H one occurs near the middle of the floor of the gut; others appear in mesoderm and others still in ectoderm. In these several regions they are seen to undergo division, losing more and more of their appearance as megaspheres (*v.* fig. 71 P). It can not be believed, therefore, that these elements are to be regarded as primitive ova, destined to carry the segregated germ plasm into the embryonic genital folds, for this would involve a conception of primitive ova traveling about extravagantly, from the gut wall to the rim of the blastoderm, a conception the more improbable when we consider that the urogenital region, to which primitive eggs naturally belong, is already indicated by this stage, as at *a*, fig. 71 G. On the other hand, it follows, I believe, that the evidence provided by Chimæra strengthens materially the position of Rückert that the megaspheres in elasmobranchs are to be regarded not as primitive ova but as highly specialized bearers of nutriment, capable of carrying into the midst of embryonic tissues centers of new formative energy. These as single large cells could be passed through the intervening tissue more effectively than could the many small cells to which they give rise, for the resistance of an embryonic tissue to the penetration of cells is obviously proportioned to the surface-contact of the invading cells.

the germinal wall, next having just emerged from the germinal wall, and finally having almost passed through the niveau of the yolk-entoderm. We have even data indicating how the upward migration of such a megasphere takes place. One sees in L a line of vacuoles appearing between the megasphere and the yolk-entoderm, and it follows clearly that the vacuoles, by a process of coalescence, provide a less resisting space into which the megasphere can rise.

Regarding, in the next place, the fate of the megaspheres, I think that there can be no doubt that they serve to bear nutriment to the tissue which they enter. In some cases, as in fig. 71 P, at *y*, they undergo mitotic division (after having divided only by amitosis in the yolk), and their descendants can not be distinguished from the neighboring cells. In other cases, M and N, they become closely surrounded by cells, entoderm in the present case, which form around them a syncytium, and appear to serve as nutriment distributors; witness for example the grouping of the cells around the large megasphere in M, and the radiating arrangement of the cells adjacent to the cluster; even the ectoderm is budding off a cell at the point nearest the megasphere.

In a word, I think we can fairly conclude that in Chimæra, even in this late stage, cells are constantly being added to the blastoderm from the germinal wall. This condition maintains in the case of the megaspheres, as we have just noted, and it holds equally good for other types of cellular additions to the blastoderm. We thus observe in O (a detail of section G) that between the yolk-entoderm (*yc*), and the wall of fine yolk (*y*) is a vacuolar zone,* in which merocyte elements are being ferried over to become cells of the blastoderm; thus at *v'* is a vacuole into which the merocyte (*m*) is about to pass. It is to be noted, however, that cells may also appear in the finer yolk, and thence by the mediation of an enveloping vacuole be passed upward into the vacuolar zone, thence to the blastoderm (*cf.* in fig. 71 O, at *m'*).

That throughout these stages there is a general transformation of the yolk from coarser elements into finer elements there can be no question. Deep in the yolk appear nuclei surrounded by spherical masses of finer yolk, in turn surrounded by masses of coarser yolk, in turn more or less irregularly by a system of vacuoles (= intercellular spaces) fig. 71 K. There is, to be sure, a greater or less amount of coalescence of these yolk elements, and in the zone close to the entoderm we observe that the nuclei with their surrounding fine yolk have come to merge into a single layer (= the zone of merocytes of the subgerminal wall). It is from the elements of this layer in turn that some cellular additions to the blastoderm are made.

The nuclear changes which occur during the process of their "levitation" are worthy of especial comment, for while the cells of the yolk-entoderm now divide by mitosis (as in O), the nuclei of the region below the vacuolar zone divide amitotically,

*Similar conditions have been observed in the early stages of teleosts (*cf.*, among others, Hoffmann, Zeit. wiss. Zool., vol. XLVI (1888), pl. XXXV, a paper, by the way, which is too little referred to in recent work on teleostean embryology).

and under varied and striking forms—albeit in a series more or less gradational (*i. e.*, showing more decided mitotic character) as one passes from a lower to a higher zone in the yolk substance. To illustrate various types of division: In R, in a sphere of fine yolk is a nucleus about to divide amitotically*; in S a similar nucleus has undergone such a division, in this case four nuclei resulting. In a somewhat similar case, T, noteworthy growth in two of the resultant nuclei has occurred; they have, in fact, passed out of the sphere of finer into the coarser yolk. In U three similar and large nuclei result. In V, which represents a later stage of the condition shown in T or U, and is drawn similarly from deep in the yolk region of a section (*e. g.*, as seen at several points in K), continued amitosis occurs; here one of the larger nuclei, especially, is seen to be budding off a small nucleus, and it has already apparently budded off several. In W, a similar detail indicates the great rapidity with which nuclei may arise; a large nucleus at one point has given off a small one, while at a neighboring point almost simultaneously (judging from the close position of the small nucleus) it is budding out a long process which is about to be separated not into a single new nucleus but into two. In X seven nuclei have arisen from a single center (? sphere substance) in the fine yolk, and of these one has undergone rearrangement in its chromatin material. Of this a dense mass occupies the center of the nucleus and is connected with the nuclear wall by a series of radiating linin strands. In Y a somewhat similar nucleus is shown in detail; at one side it is apposed to the finer yolk (= ? sphere substance) and here the mass of chromatin approaches, indeed almost touches the nuclear membrane (for nutritive reasons?). In another nucleus, Z, the chromatin mass shows a doubled arrangement, preliminary, as it appears, to a stage in division shown in AA, FF, and possibly in BB. In turn the doubled nucleus in CC is obviously a further stage than AA, but it shows also around it a series of (five) smaller nuclei which, from their radiating arrangement around the dividing nucleus in the center of the fine yolk, are possibly the descendants of a similar type of nuclear division. In DD a nucleus shows a less distinct doubling of its chromatic elements than AA–CC. And in EE a distinct threefold division occurs. GG represents a stage in division carried further than CC, the neighboring nucleus having probably arisen from a similar division. In HH are two neighboring nuclei, the products, we conclude, of a division like that of GG and CC: but, curiously enough, they are undergoing division in different ways. The upper, near which appears an attraction sphere and centrosome, has arrayed its chromatin in two masses nearly equal in size, each suggesting a confused series of chromosomes; the lower is simply passing out a portion of its chromatic substance into the fine yolk. In II, the last of the series given, two nuclei appear; they are evidently products of such a division as GG, and each in turn is about to undergo division. The lower one is noteworthy, since the division of the chromatin material is practically completed in the middle of the nucleus. It may be said in general that the nuclear processes which here approximate mitosis (CC or HH) are observed in the region immediately subjacent to the yolk entoderm.

*A similar condition in the embryonic germ cells of Loligo appears to be due to rapid growth, and is not followed by fragmentation (Miss Sturges, Science, 1899, Feb. 3, pp. 183-184).

In summary: The evidence which is thus provided strengthens the conclusion that in the gastrulation of Chimæra amitosis is not to be interpreted in accordance with the current view, *i. e.*, as a process of decadent cell division. It is conditioned, rather, by rapid growth and multiplication of nuclei, since its products may resume mitosis when the usual rate of cellular division is attained. Moreover, the products of amitotic division in the blastoderm of Chimæra, are too many and too widely scattered to warrant the belief that their cellular descendants can play no part in producing permanent organs

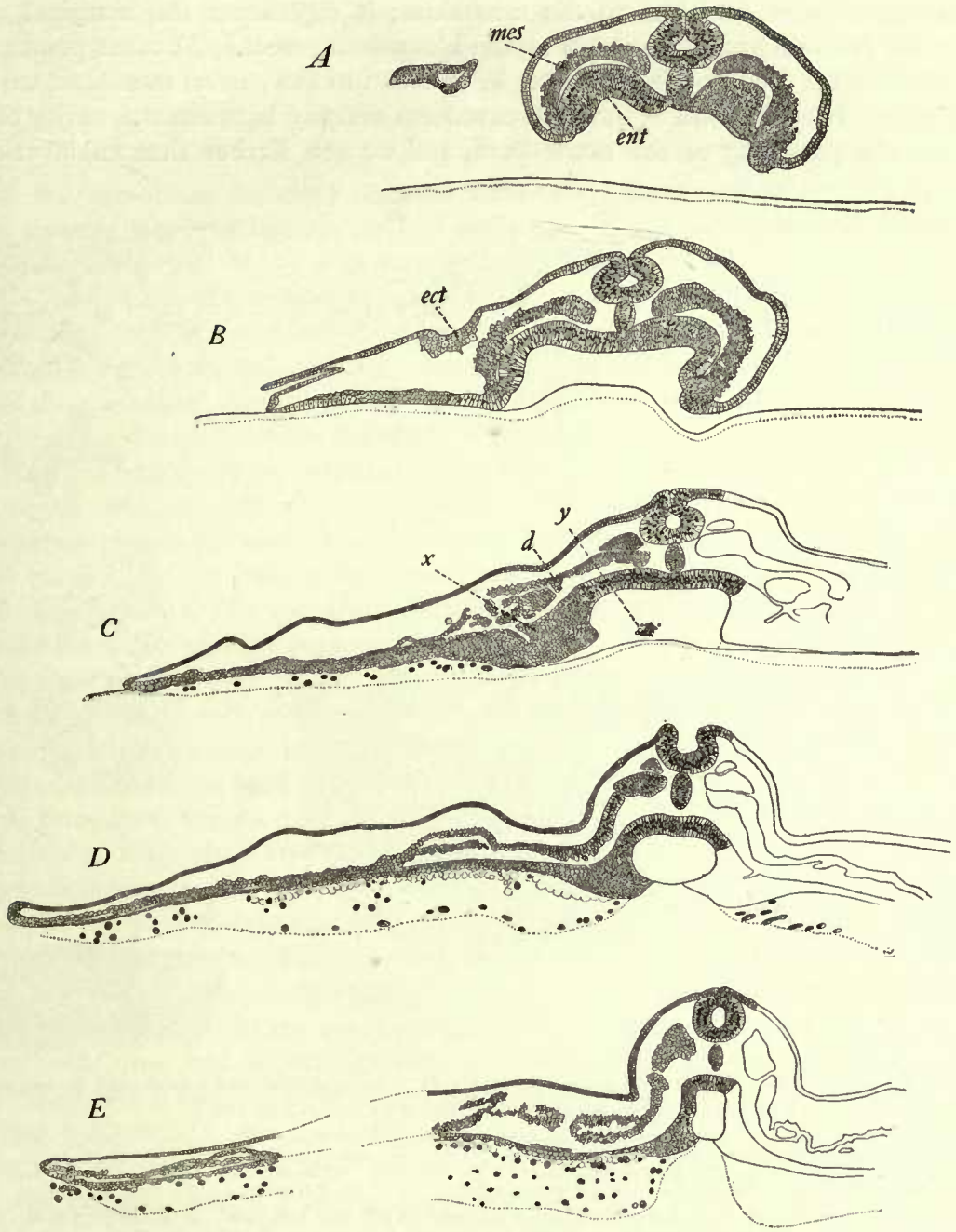
Later Gastrula. Embryo With Partly Closed Medullary Folds.

This stage is figured in surface view, plate v, fig. 37, and enlarged, viewed as a transparent object, in plate vi, fig. 41. It corresponds approximately with Balfour's stage f in the shark.

Comparing the blastoderm of this with the preceding stage, we find that it has increased but little in size. The spongy region, however, which occupies its central portion appears more prominently, and we observe a noteworthy thickening in the region of mesoblast (gastral) extending outward on either side of the embryo. The details of the embryo are well seen in a *toto* preparation. The medullary folds arch over and meet in the median line, fusing in the posterior third of the embryo's length. In front of this, after a slight interruption, the folds meet again, then diverge to a degree suggesting the corresponding stage of shark. The tail folds are conspicuous at this stage, and we observe that the gut has arched upward, a transverse line showing where a neurenteric canal is to open below. On either side in this region the mesoblast is thickened, fading away laterally. Here are forming the extensive caudal veins. Other vascular details are shown in the antero-median vessel (apparently vitelline vein) which appears immediately in front of the head and spreads out widely over the blood-producing region. We note also transverse larger vessels, the vitello-intestinal, extending outward on either side to about an equal distance. Gastral mesoblast is conspicuous in this stage; in this may be traced about a dozen somites, the anterior ones extending far forward.

Details of Foregoing Stage, Corresponding to Balfour's Stage F.

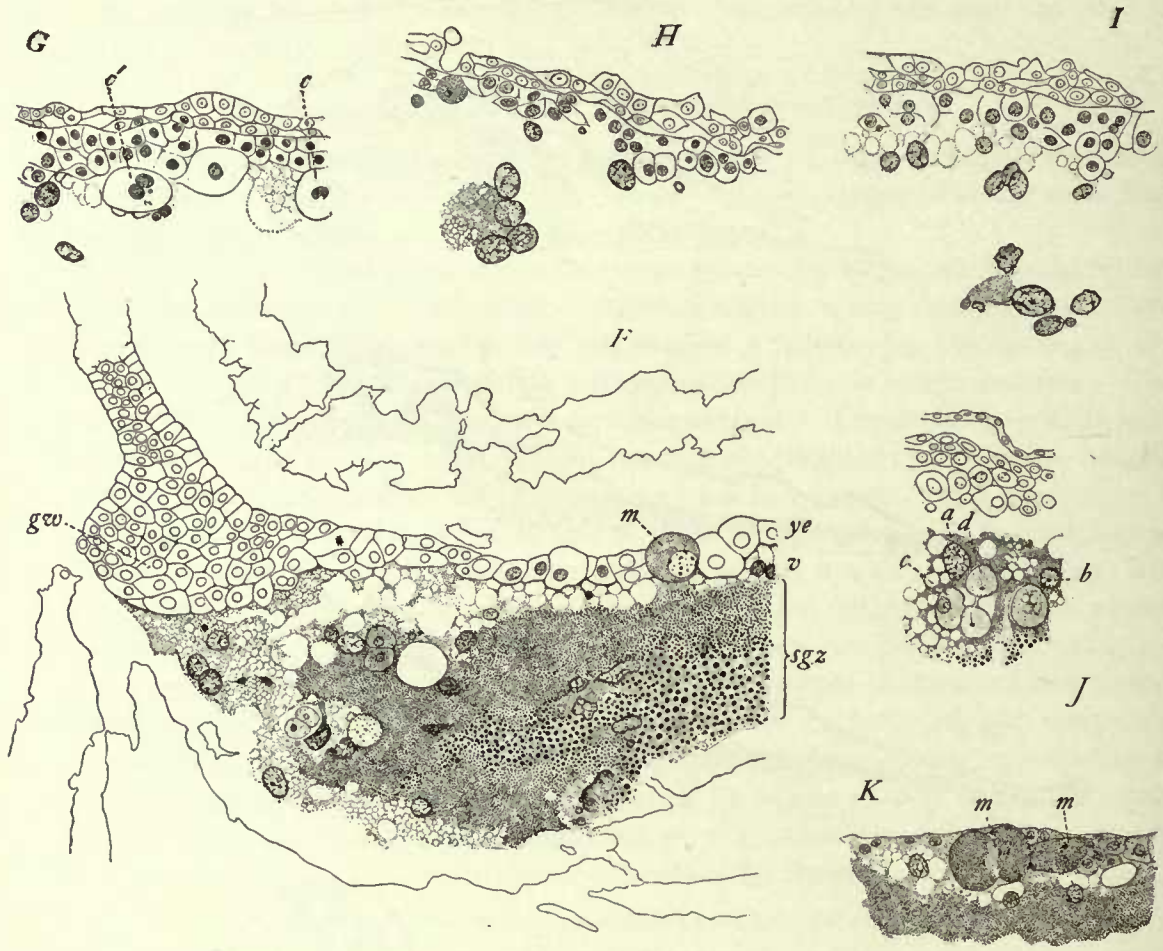
Sections are shown in fig. 72 a–e passing through the blastoderm in a plane transverse to the axis of the embryo. In the first, which passes through the tail region of the embryo, we observe that the mesoblast bands (*mes*) are continuous with the entoderm not in the region adjacent to the notochord but marginally (*cf.* the view of Graham Kerr as to this place of origin in the vertebrate gut pouches); near by the entoderm (*ent*) thickens conspicuously, then thins again as it passes into the notochord. Only at the open notch between the tail folds does the lumen of the nerve tube pass over into the wide space (*cf.* fig. 71 a) which is coming to form the cavity of the gut. It will be seen that it is especially the thickening of the entoderm and the constricted origin of the mesoderm which in the transparent preparation (plate vi, fig. 41) causes the appearance of a dark band in the region of the tail folds of the embryo. In fig. 72 b similar conditions in gastral mesoblast and



Figs. 72 A–E.—Transverse sections and details of the blastoderm shown in fig. 72. The sections pass anteriorward from the region of the caudal folds, shown in section A, as far as the "neck" region of the embryo, section E.

d. Beginnings of segmental duct.
ect. Ectoderm at the point where this becomes continuous with the mesoderm in the tail folds of the embryo.
ent. Entoderm.
mes. Mesoderm.
y. Yolk lying free in the gut cavity.
x. Urogenital aolage.

entoderm prevail; the thickened ectoderm at *ect* marks a point at which this layer is making cellular additions to the mesoblast; it represents the marginal point where the tail fold and the margin of the blastoderm meet. At other points also, the mesoblast is receiving increments; in addition to the gastral mesoblast we note cells arising from the wall of the yolk-entoderm midway between the cavity of the gut and the periphery of the blastoderm, and we see further that an invasion of



Figs. 72 F-K.—Details of the region of the yolk-entoderm of fig. 72. In *F* the region is indicated in detail which lies immediately below and at the side of the arching wall of the gut. (Cf. fig. 72 E.)

a. Large vacuolar nucleus which appears on the point of undergoing reconstitution into a cell of the yolk-entoderm.
b. Nucleus similar to foregoing, but in a less advanced condition.
e, e', *d*. Cells which have recently been differentiated out of the germinal wall.
m. Megasphere.
sgz. Subgerminal zone.
v. Vacuolar zone.
ye. Yolk entoderm.

G, H, and I illustrate particularly the zone of reconstruction of yolk-entoblast cells from yolk nuclei. In J a telophase occurs, representing a rare condition in the subgerminal zone. In K, similarly, a telophase occurs in a megasphere. The latter has, however, passed through the zone of vacuoles and lies in the yolk-entoderm. In this neighborhood, however, as we note at the left, a syncytial condition may be present.

cells from the periphery of the blastoderm has occurred, in the form of a crease-shaped invagination. In c the dorsal wall is sharply distinguished from the sides of the gut. On the floor of the latter appear small masses of yolk, *y*, which can only serve, as already noted, as ingested nutriment. The mesoblast in this region shows considerable differentiation; myotomes are sharply marked off; the gono-

nephrotomal zone is of notable size; at *d* and in the adjacent cell-mass (at the left) are the beginnings of the pronephric tubules; and below at *x* appears the thickening of the mesentoderm whence arises the posterior portion of the pronephric duct.

In a section, D, passing through a more anterior region of the embryo, the urogenital structures are practically undifferentiated; the mesoblast extending continuously from the notochord to the periphery of the blastoderm. In this region the mesoblast probably receives little or no increment from the yolk-entoderm, judging from the latter's smooth surface, save only at or near the margin of the blastoderm. Below the yolk-entoderm in this region the subgerminal zone of nuclei is more conspicuous and definite than in the early stage, fig. 71 E, and this zone, indeed, appears with even greater prominence in the more anterior section, fig. 72 E (to be contrasted with fig. 71 F or G). It will here also be seen that division of the mesoblast into splanchno- and somatopleure is occurring, and that the lateral wall of the gut is more definitely established.

A detail, shown in F, indicates the more special relation of the subgerminal zone to the marginal cells of the gut cavity. The subgerminal zone is here reduced to a narrow tongue (*cf.* also E), which inserts itself under the thickened mass of cells at the base of the gut wall, in the direction of the lumen of the gut. In the present detail the base of the gut wall is shown at *gw*, the yolk-entoderm at *ye*, the vacuolar layer at *v*, and the subgerminal zone at *sgz*. We note first of all the narrowness of the vacuolar layer, through the intervention of which we have seen (fig. 71 O) yolk nuclei become cells of the embryo, a condition indicating the specialization of this region. In this zone (*v*), furthermore, we see large nuclei which are evidently in transition between yolk and embryo, and at *m* a megasphere which has just passed through it, the vacuoles becoming reconstituted below. Most significant in the region of the rim of the gut wall is the concentration of the elements of the subgerminal zone, coarse yolk, fine yolk, lacunæ, vacuoles and yolk nuclei of different kinds, the continuation (to the left) of the vacuolar layer, and the compounding of its vacuoles—characters which are obviously to be interpreted as more special and complicated than in the earlier stage.

A few additional details may be cited. In G, where nuclei are passing through the vacuolar zone and becoming cells, we observe that at *c* a nucleus which has been taken into a large vacuole (a process forming now a reconstituted cell), is still dividing amitotically, and that at *c'* a similar division has recently occurred, indicating in both cases, as we have before remarked, that the difference between amitotic and mitotic division is one of degree rather than of kind. In H, a detail from a section close to fig. 72 E, a point is figured where merocytes and newly constituted yolk-entoderm cells occur in such confusion that it is difficult to say where the layer of merocytes terminates and where the cells of the embryo begin. And the same is true of the detail shown in I. In the last figure, on the other hand, merocytes are still multiplying, even at a point close to the yolk-entoderm. In J, a detail of the vacuolar region, cells are arising from merocytes; at *b* a merocyte, less vesicular than *a*, adjoins a vacuole into which it will probably pass, judging from transitional conditions (*cf.* the neighboring c). And even in the vacuolar layer such newly

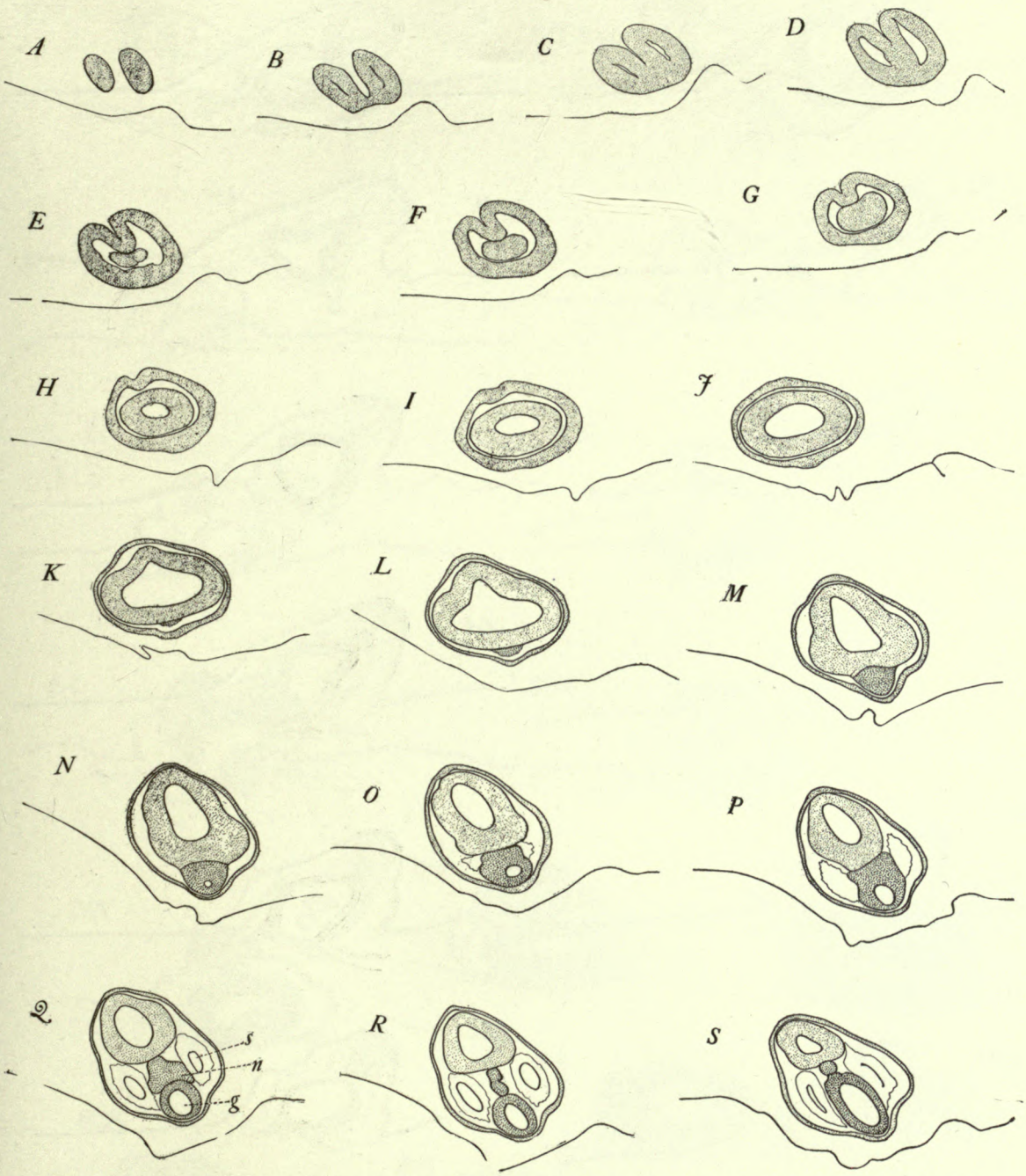
constituted cells may divide, and by mitosis, although this is not of the usual type (*cf.* at *d*). In this connection, finally, in K a detail is given showing that megaspheres as they pass into the yolk-entoderm present more or less evident mitosis, witness the conditions *m* and *m* (*cf.* also fig. 72 F at *m*). Parenthetically, just below the megaspheres here mentioned are vacuoles into which merocytes are passing.

EARLY EMBRYOS FROM THE COMPLETE CLOSURE OF MEDULLARY FOLDS TO OPENING OF GILL-CLEFTS.

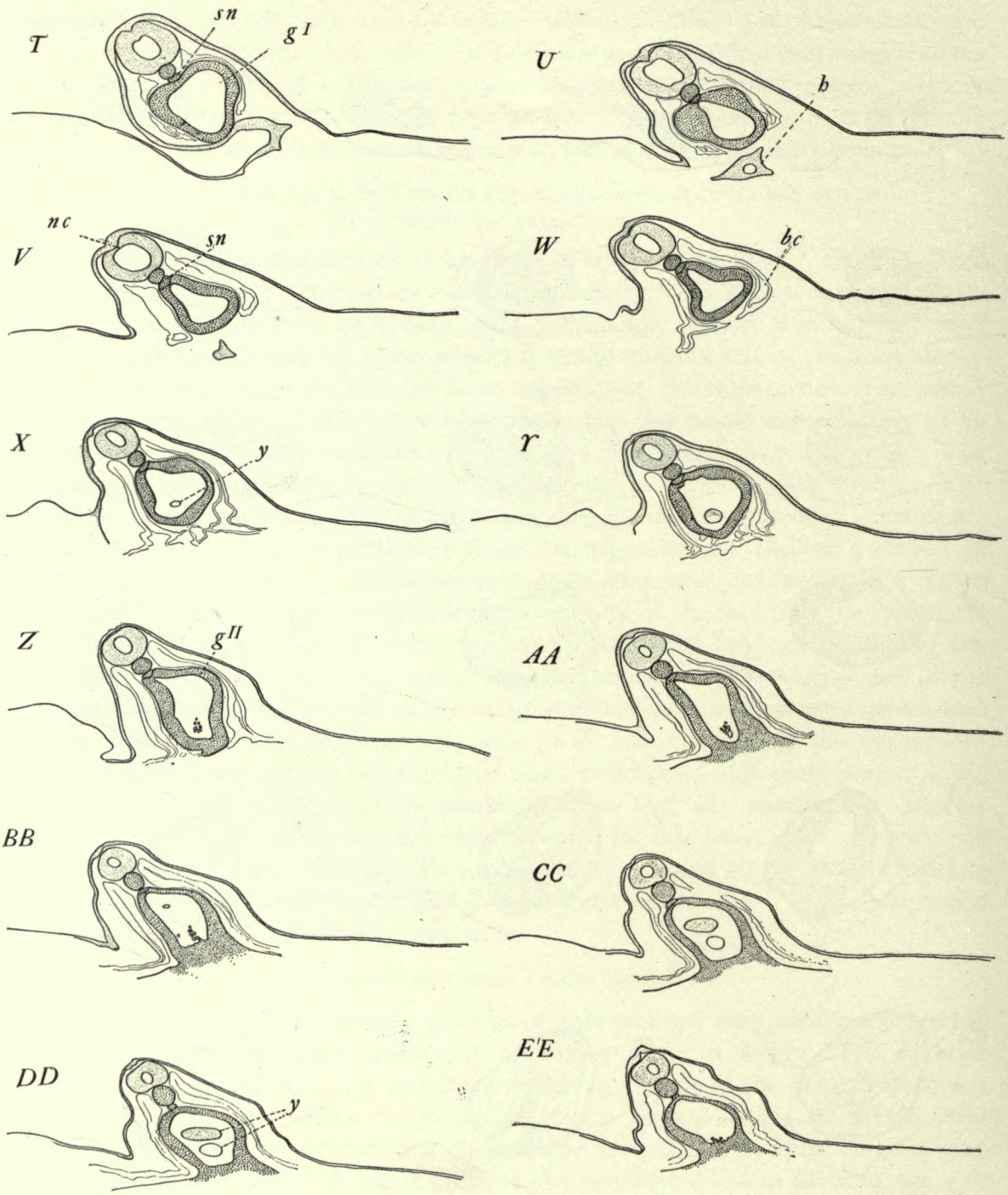
An early embryo attached to its blastoderm is shown in plate V, fig. 38. This may be contrasted with the stage of closing medullary folds shown in same plate, fig. 37. In the blastoderm we observe that the spongy central area has increased notably in size and that it has even extended to the anterior rim of the blastoderm. We note also that asymmetry has made its appearance, the embryo now lying somewhat on its right side. The present blastoderm has increased more rapidly at its left, and here a lobe-like eminence is produced hindward over the yolk. The entire size of the blastoderm is scarcely larger than in the preceding figure. The embryo is shown in detail, plate VI, as an opaque, fig. 41[a], and then as a transparent object, fig. 41[b]. In general this stage corresponds with Balfour's stage G in shark; it differs, however, in the definiteness of its structures, for the anterior region has already become quite highly differentiated in spite of the fact that the tail region is still flattened out against the yolk and hardly protrudes beyond the rim of the blastoderm. About 22 segments are present in this stage. The head rises above the blastoderm and the divisions of the brain and the optic vesicles are formed, and it is an evidence of the high specialization in development that the embryo of this large-eyed form should possess large optic vesicles at this early period, *i. e.*, before the tail end of the body is established,—a fact of considerable interest from the standpoint of embryonic adaptation. In this stage two gill-slits are appearing, g^{I}, g^{II}. The region of the pronephros is marked out at *pn*, the heart at *h*, the anterior cardinal vessels at *c*, and the vitello-intestinal at *o*. In the tail region the neurenteric canal is distinctly seen at *n*.

Details of the Present Embryo (Stage G).

A series of selected transverse sections of this embryo may now be passed in review to indicate the more prominent advances, figs. 73 A–UU. The anterior sections A–D pass through the ectoderm inclosing the tip of the head and show a conspicuous median infolding (recessus olfactorius impar) which in surface view gives the appearance of separating a "forebrain" from a "right optic vesicle," the sections having been cut in the plane indicated by the dotted line in plate VI, fig. 41[b]. The next section (E) touches the distinct end of the central nervous system, the wall of which is more extensively traversed in F and G. In H, I, and J, the lumen of the forebrain is traversed. In K and L, representing many sections, the cavities of the optic vesicles appear, and we observe here closely apposed to the ventro-median wall of the brain a mass of cells which in later sections is seen to constitute the anterior end of both notochord and gut. In sections M and N this cell mass forms a conspicuous ventral keel, in N the lumen of the gut first appearing. In O and P

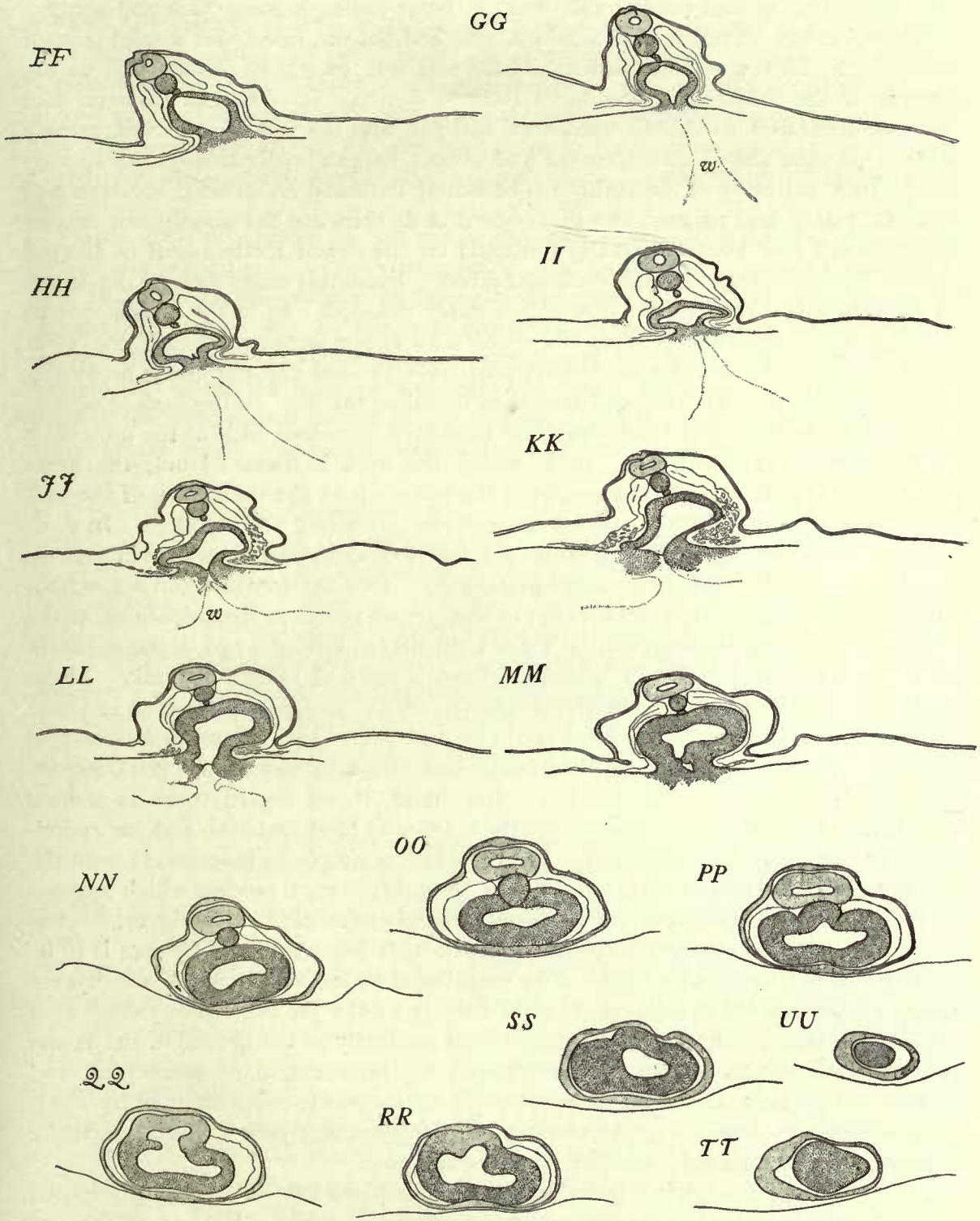


Figs. 73 A–S.—Transverse sections of embryo shown in plate V, fig. 38, and in plate VI, figs. 41 and 41 A. These begin at the head end of the embryo, section A, and extend through 47 sections to the tip of the tail, section UU (see pages 94 and 95.)
g, Gut cavity; *n*, notochord; *s*, somite.



Figs. 73 T-EE—Continued.

bc. Body cavity.
g^{I}, g^{II}. Evagination of gut wall to form the first and second gill openings.
h. Heart.
nc. Neural crest.
sn. Subnotochordal rod.
y. Yolk lying free in cavity of gut.



Figs. 73 FF-UU.—Continued.

w. Wedge-shaped mass of yolk which comes to pass into the ventral wall of the gut cavity.

we distinguish in this ventral cell mass a lower lumen-bearing area and above a thickened mass, on either side of which, attached but not fused, lies a solid mass of mesoblast. In Q we distinguish notochord and gut (*n*, *g*); on either side of the notochord the mesoblastic somite (*s*) bears a cavity. In R the mesoblastic sacs are well separated from both notochord and gut, and the notochord itself, greatly reduced in size, shows a compressed and almost longitudinally subdivided appearance. In S, the body of the embryo is becoming flattened on its side; the lumen of the gut is deep and narrow; closely apposed to its sides are the mesoblastic masses whose lumen now becomes greatly reduced; on the dorsal median wall of the gut appear the beginnings of a subnotochordal rod. From this stage onward the lumen of the central nervous system becomes notably reduced. In T the section passes through the embryo in the plane where the neck region flattens out over the yolk. Here we note the distinct subnotochordal rod (*sn*) and the flattening mesoblast which now forms a delicate band almost surrounding the gut. In the surface view of this region, on the other hand, only the thickened proximal ends of the mesoblast masses can be distinguished. In U, where the neck is flattened out, the heart appears at *h*; and in the upper region of the gut we note the thickening of the wall of the gill-slit, the cavity of which is seen in the preceding section at g^{I}. In V, as indeed in some of the earlier sections, a thickened neural crest appears at *nc*. In W the body cavity (*bc*) is becoming conspicuous. In X the somato- and splanchnopleure spread out widely peripherally; in the gut we notice in the thickening of the lateral walls an out-bending for the second gill-slit (*cf.* in Z, g^{II}) and in the cavity of the gut in this and in many sections following we find masses of yolk. These masses, sometimes small, as in sections Z, AA, BB, EE, sometimes large, as in Y, CC, DD, are unquestionably budded out (as in EE and HH) of the ventro-median wall of the gut. On account of their abundance and range in size we can not conclude that they are artifacts, but, on the other hand, if we regard them as normal structures, it is natural to assume that they serve as food material, and are assimilated by the gut in the usual way. This conclusion, simple as it seems, is none the less difficult, since it attributes to Chimæra an embryological process which appears to be unknown in the vertebrata and only remotely paralleled among invertebrates. If, accordingly, we accept the present evidence, it follows that Chimæra is to be regarded as the terminal member of an evolutional series, at one end of which were forms whose yolk-laden cells contributed directly to the growth of the young; next came those whose yolk-filled cells contributed indirectly to the growth of the young through various processes, typically through the intervention of merocytes; and finally, in Chimæra, the mode of nutrition by merocytes is supplemented by a still more oblique process, *i. e.*, one which passes fragmented yolk material from the zone of merocytes directly into the lumen of the gut.

Continuing the sections: In GG, and in many sections following, a wedge-shaped mass of yolk material (*w*) is converging toward the ventro-median line of the gut (*v.* also p. 76); in LL it becomes subdivided, and in MM appears a small recess which may also contain this nutriment (? anlage of liver). In JJ and in following

sections the pronephric duct appears, at first only on the left side, as an ectodermal keel, beginning about the plane of the 8th somite. Thence, passing backward, it merges with the somatopleure at about the plane of the 12th somite, after MM. In this section the subnotochordal rod appears for the last time. In OO the notochord dips into the dorsal wall of the gut; and in PP it forms an evagination of its wall. QQ and RR are sections through the neurenteric canal, and SS to UU through the tail end.

Two further details of this stage are shown in figures 74 and 75. The former of a section close to that of fig. 73 LL, the latter from a section close to fig. 73 G, representing only a detail of the extra-embryonic blastoderm lying under the region of the head. Fig. 74 has been given to illustrate the ingress of yolk material through the ventral wall of the gut, for here is seen the wedge of yolk protruding through the thickened mass of yolk-entoderm cells, but under conditions which bespeak the complicated nature of the process. For the rest, there is here not a mere rupture which admits the yolk into the cavity of the gut, but an attendant

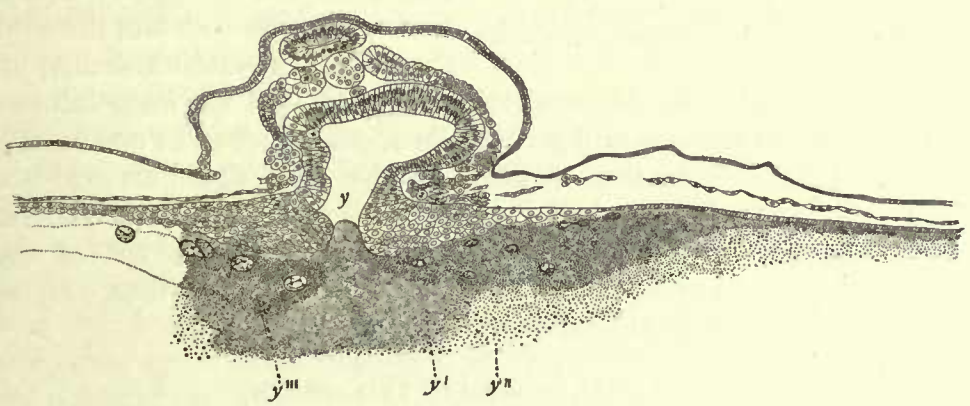


Fig. 74.—Detail of section of early embryo shown in fig. 73 LL.

y, Yolk plug pressing into cavity of gut; y', y'', y''', layers of yolk of different consistencies.

series of changes of which the "rupture" itself is, with fair probability, the terminal member. Thus the wedge-shaped mass of yolk (y) is composed of fine yolk; it next passes through a transitional zone (y') into the coarse yolk (y''). And on either side of the wedge lies a layer of very coarse yolk (y'''), which obviously comes into close physiological rapport with the neighboring layers, for this thickens as it approaches the yolk-wedge, and here it is filled with nuclei of extraordinary size. Indeed on one side (left) we note that this layer of coarse yolk is separated from the yolk-entoderm by a layer-like offshoot of the fine yolk (y') from near the point of the wedge. We observe also the relation which the bordering yolk-entoderm bears to the point of the yolk-wedge, for this layer is here many times thicker than in neighboring regions. The yolk-wedge, in short, which passes into the cavity of the gut stands in specialized relation (1) to the usual mass of yolk, *i. e.*, spreading out fan-shaped below, thus securing a large surface of contact; (2) to the lateral areas of coarse yolk; (3) to the lateral masses of yolk-entoblast, and (4) finally, as we

have already seen, to the walls of the gut, since it passes to them yolk masses, large and small, and perhaps also dissolved yolk material. In evidence of the nutritive value of this material witness numerous mitoses in the adjacent (inmost) cells of the entoderm—one of which appears in the present section.

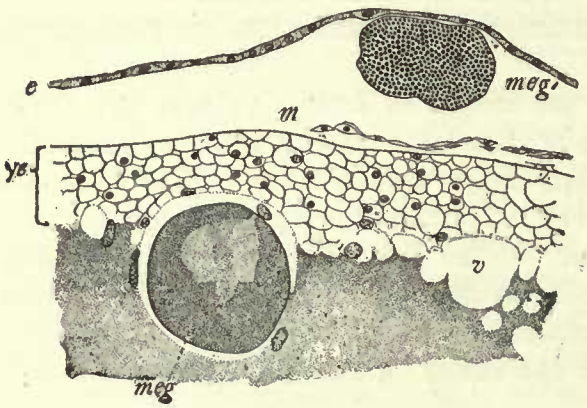


Fig. 75.—Detail of extra-embryonic region of embryo of fig. 73. *e*. Ectoderm; *m*, mesoblast; *meg*, *meg'*, gigantic yolk-cells; *v*, vacuole; *ye*, yolk-entoderm.

In fig. 75 a detail is given of the process by which yolk-cells are passed into the tissues of the embryo. In this portion of the extra-embryonic blastoderm the mesoderm occurs only as detached (mesenchymatous) cells (*m*); the ectoderm forms a single-celled layer, and the entoderm a closely formed cellular mass (*ye*). Between the entoderm and the yolk is the usual zone of vacuoles (*v*). At *meg* a large yolk-filled cell (*cf.* pp. 83 *et seq.*) protrudes from the yolk into the entoderm, the cells of the latter affording little bar to its progress upward. In this connection we note that the huge cell (*meg*) lies now within a vacuole in whose wall yolk-nuclei appear; indeed at one point a yolk-nucleus has actually entered the vacuole. In the same figure at *meg'* is a large cell (cut not quite through the middle) which has evidently had a similar origin to *meg*; for from its size it can not be confused with a neighboring cell of any germ layer. It contains coarse yolk, and on account of its irregular outline, judging from earlier instances, it has probably undergone division by amitosis.

ADDITIONAL EMBRYOS OF THIS PERIOD.

A second embryo of this period, *i. e.*, prior to the breaking through of gills and mouth, is shown on plate VII, figs. 42, 42^a and 42^b, and on plate VIII, fig. 42^c. The present specimen is badly bent in its trunk region, but in other regards it may be readily compared with the earlier stage, plate VI, fig. 41. The chief advances include: (1) the modeling of the trunk, in whose hindmost region only appears the former flattened condition; (2) the appearance of auditory sacs (*au*); (3) the modeling of optic vesicles (*op*); the protrusion of the forebrain region into a frontal knob (*k*). The general shape of the head, as shown in dorsal view, already suggests the adult condition, in spite of the small size of the embryo. This now measures only 2.5 mm., not allowing for the bent trunk region. The tail at this stage protrudes beyond the rim of the blastoderm, its tip budding out like a knob beyond the flattened caudal eminence. About 25 somites are present.

A third embryo, plate VII, figs. 43 and 43^a, shows over sixty somites, and gives us a picture of the young Chimæra at about the end of the first month of incubation. In this stage over sixty somites are present, and the tail bud has

grown out conspicuously. The broad flattened trunk terminal of the preceding embryo is here represented, and at *a* the anal region, a point anterior to which the number of somites corresponds in a general way to that in the earlier stage. Noteworthy advances include:

(1) A more definite modeling of the regions of head and trunk. The latter has now lifted up above the surrounding blastoderm, and the head (including the chin region) has separated from the yolk-wall.

(2) The gill-slits are now conspicuous, although, as sections show, they have not yet broken through; we note that the spiracular slit *s*, evidently the equivalent of g^1 in the former stage, is of considerable size; behind it occur three prominent depressions and the trace of fourth and fifth.

(3) The appearance of pronephros and pronephric duct; the pronephros itself is situated at the plane of the ninth, tenth, eleventh and twelfth somites, as can better be seen in the transparent preparation in the same embryo, plate VII, fig. 43^a.

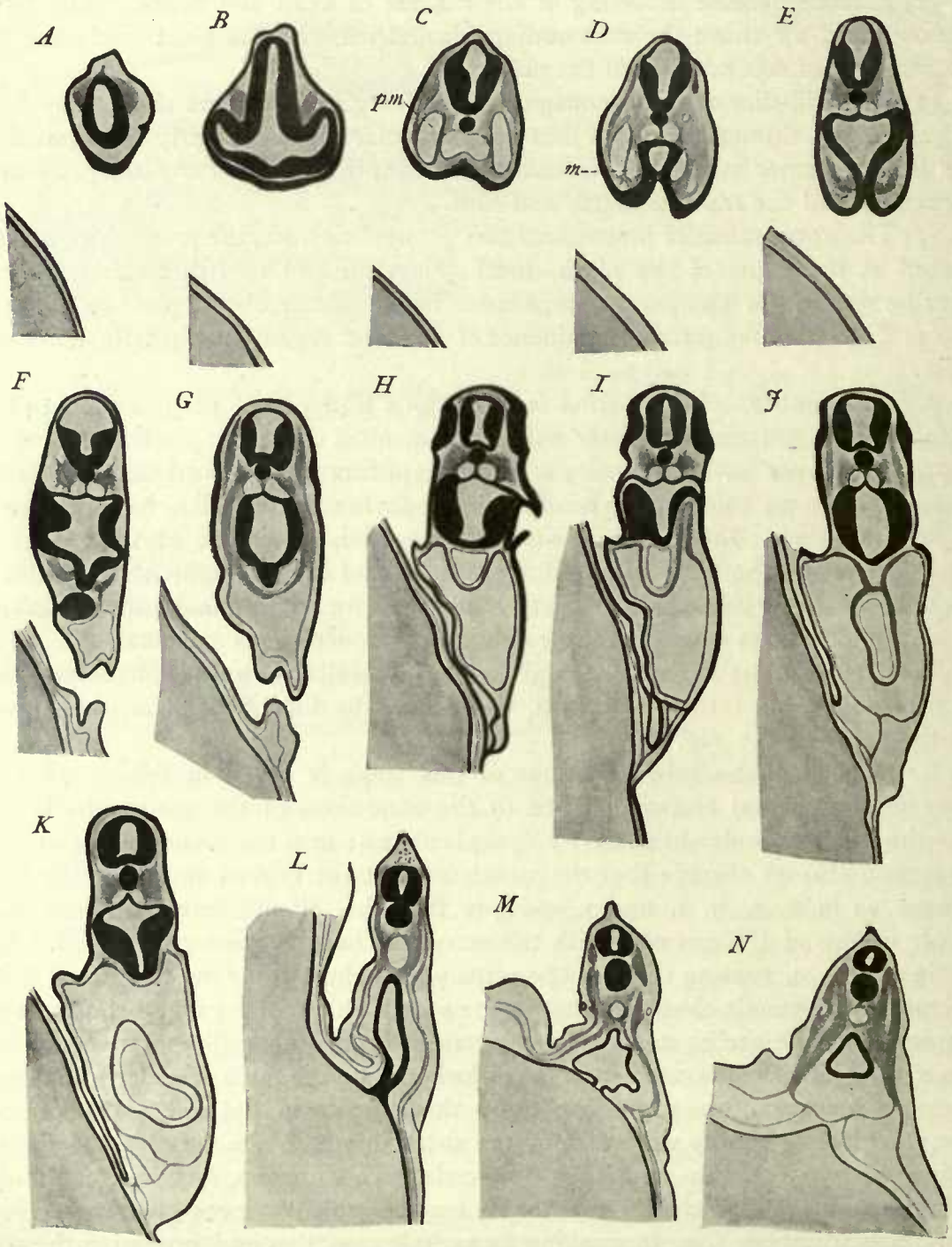
(4) The knob-like terminal eminence of the head region has greatly increased in size.

A fourth embryo of this period is shown as a transparent preparation in plate VII, fig. 44. It contains a greater number of somites than the preceding, over 80 as opposed to over 60, but in many regards it appears to be less advanced in development. Thus we note that its head region appears somewhat less mature than in the former embryo; the chin is less definitely established and so also the gill-slits are shallower and the optic and auditory vesicles and the pronephros less definite. The tail, moreover, is less pointed, even bulbous where the terminal growth is taking place. In this stage we note the presence of a conspicuous postanal gut. The details of the vascular supply of the gill region are well shown; the spiracular artery is conspicuous, and, further hindward, we observe the duct of the pronephros (*pnd*) and the postanal gut *pag*.

A series of characteristic sections of this stage is given in figures 76 A–N. These show a general correspondence to the conditions of the young shark. In fig. C the premandibular head cavity (*pm*) is shown; in D the mandibular (*m*). In this section also we observe that the mouth has not yet broken through. In later sections, as in E, F, H, I, and K, we note that the gill-slits have not been completed; fusions of the gut wall with the ectoderm have, however, occurred. We note in section M, passing through the pronephric tubules, that the relation of these structures corresponds closely to that in the young shark. A subnotochordal rod, conspicuous in the earlier stage, is here represented only in a rudimentary condition, as in N; the gut has separated from the notochord and the main vascular trunks now appear in the region formerly occupied by the subnotochordal rod. The present stage corresponds closely with that of the shark in which the mesoblast bounds a continuous myo-, nephro-, and splanchno-cœle. In Chimæra, however, continuity in these regions is less clearly marked, a feature which evinces greater developmental specialization, *i. e.*, in masking an archaic condition and preparing the way for the prompter growth of structures useful to the young fish.

THE RELATION OF THE BLASTODERM AND YOLK AT THIS STAGE.

As already noted (p. 58), the egg of Chimæra has by this time undergone a process of fragmentation. The bulk of the egg subdivides in the direction of producing for the embryo nutriment to be appropriated *via* gills and gut; a single mass



Figs. 76 A–N.—Transverse sections of the embryo shown in plate VII, fig. 44.
m, Mandibular head cavity; *pm*, premandibular head cavity.

only, representing about one-tenth the bulk of the unsegmented egg, is reserved for the yolk-sac of the young fish.

In the stage last described (*i. e.*, of plate VII, fig. 44), in spite of the advanced characters of the embryo, the blastoderm has not increased vastly in size beyond that shown in plate V, fig. 38. It has, however, as we see in plate VIII, fig. 47, constricted marginally, becoming cup-shaped, as it continues to envelop the small yolk mass. How far it has succeeded in inclosing the yolk is perhaps better seen in the details of the last figure, shown in figs. 47[a] and 47[b].

The relation of yolk and blastoderm is pictured in detail in fig. 77, a section passing through the blastoderm parallel to the long axis of the embryo. At the points *mb* and *mb'*, the rim of the blastoderm comes in contact with the yolk; above *mb* the blastoderm is thickened and spongy; for, as a sign that the body of the embryo lay adjacent, this region is richly vascular. Noteworthy here is a deep submarginal sinus (*ms*) whose posterior wall (*c*) is cellular. We have in this condition a physiological parallel with the submarginal space in ganoids, and more directly even with Kupffer's vesicle in teleosts. On the ventral side of the blastodermic cap (on the left in the figure) the vascular sponginess is largely lost; and the blastoderm is thin, save only at its rim (*mb'*). And here in place of a deep submarginal sinus, a number of distinct blood-producing vesicles appear (*ms'*) scattered distally in a narrow zone of finely divided yolk (*fy*). From another standpoint, finally, the present section is noteworthy. For it shows that the entire yolk-sac is divided into masses which are largely separated from one another by a system of fissure-like vacuoles. Closer inspection shows nuclei scattered irregularly through these masses of yolk, and, everything considered, I think we can therefore justly conclude that the yolk-sac at this stage, in spite of its relatively large size, is a totally segmented structure comparable with the yolk-sac of Amia or Ichthyophis. In the present case, it is true, the yolk masses (blastomeres) show a condition of greater or less attachment to their neighbors, and each mass will usually contain more than a single nucleus. But even in this event, the comparison will, I believe, hold. In some cases the shape of the yolk masses is distinctly blastomere-like, as between the vacuoles (*v*) in the present section. Viewed from this standpoint, accordingly, Chimæra has retained a primitive embryological character, holoblastic cleavage; but we can hardly fail to observe that this character has lost much of its primitiveness inasmuch as the blastomeres are polynuclear and the intercellular spaces obviously adapted as reservoirs of nutriment.

Fig. 77.—Section of extra-embryonic region and of upper part of yolk-sac of stage of plate VIII, fig. 47.

c. Cellular area; *mb*, *mb'*, margin of blastoderm; *ms*, marginal sinus; *fy*, fluid yolk; *v*, vacuoles.

LATE EMBRYOS.

EMBRYOS FROM THE APPEARANCE OF GILL-OPENINGS TO THE TIME OF HATCHING.

Four specimens illustrating this period are described on the following pages. The first of these, shown *in toto* (plate VII, fig. 45), illustrates a stage in which all five gill-slits are clearly shown, but of these only the first has completely broken through, that lying immediately below the auditory vesicle. In front of this the spiracular cleft is faintly outlined. The entire head region is modeled clearly, and the anterior end of the embryo has separated from the blastoderm as far back as the region immediately behind the heart. The tail has greatly elongated and has entirely lost the bulbous terminal which we noted in the earlier embryo.

The region immediately adjacent to the embryo is divided up into a spongy mass by many blood-vessels; we observe also that the blastoderm has almost completely inclosed the attached yolk mass, a small yolk plug only being visible at the hinder end of the yolk-sac. This condition is shown in plate VIII, fig. 48. Here, through the rim of the blastoderm one can faintly see the extent of the submarginal sinus which was noted in the preceding stage. From it now extend many vessels, as indicated in the figure. The region of the yolk plug is figured in plate VIII, fig. 48[a], as viewed under a dissecting microscope. It shows an interesting condition in connection with the holoblastic behavior of the yolk; for a number of irregular masses are visible, outlined, it appears, by vacuoles, and suggest yolk-filled blastomeres. It will be observed, however, that the contours of the yolk masses are less definite as they approach the irregular rim of the blastoderm. (*Cf.* fig. 77.)

Sections of this stage are shown in the adjacent figures. In the first (fig. 78) the mouth (*i. e.*, its hinder portion) and auditory vesicles are traversed; the mouth has not yet broken through nor has the neighboring gill-slit, the hyomandibular. We note that the auditory vesicle is now a thick-walled sac opening broadly at the surface; that a subnotochordal rod is present; that the brain wall in this region (hindbrain) is remarkably thick and asymmetrical, and that the fifth ventricle is correspondingly reduced in diameter. A section through the mid-trunk (fig. 79) indicates that in this region the trunk is spread out more widely than in the corresponding or, in fact, in any stage in the shark. The splanchnocœle (*spc*) is of great size, and its walls, both splanchnic and somatic, contain large spaces. The myocœle is virtually obliterated, although its margining cells have not fused across its earlier opening into the gononephrocœle. The last region is not clearly demarked; at *pn* a pronephric tubule appears in the position usual in elasmobranch. At *df* the early condition of the dorsal fin corresponds closely with that of a shark embryo.

A second embryo (plate VII, fig. 46) slightly older than the preceding, was one of the specimens received from Dr. Wilbur. It had with it only a small fragment of the blastoderm, and at the time of preservation the embryo appears to have turned in a position nearly transverse to its usual one. At this stage the tail protruded widely over the rim of the blastoderm, and it follows, therefore, that, probably as an individual variation, the blastoderm has not as completely inclosed

the yolk as in the former specimen. A more detailed examination of this embryo shows that two gill-slits have broken through. The mouth, moreover, is more nearly completed, the mandible appearing and the visceral region having a more advanced contour. The pronephros is conspicuous. The pectoral fin is present as a longitudinal dermal ridge. The tail, judging from its twisted condition, is evidently capable of active movements. This, however, in its detailed structure, as shown in a transparent preparation (plate VIII, fig. 46[a]) is still distinctly immature; its tip retains a neurenteric canal (*nc*), and a postanal gut (*pag*). In the latter the irregularity at the point *x* is probably artifact. The present embryo measured about 20 mm. in length.

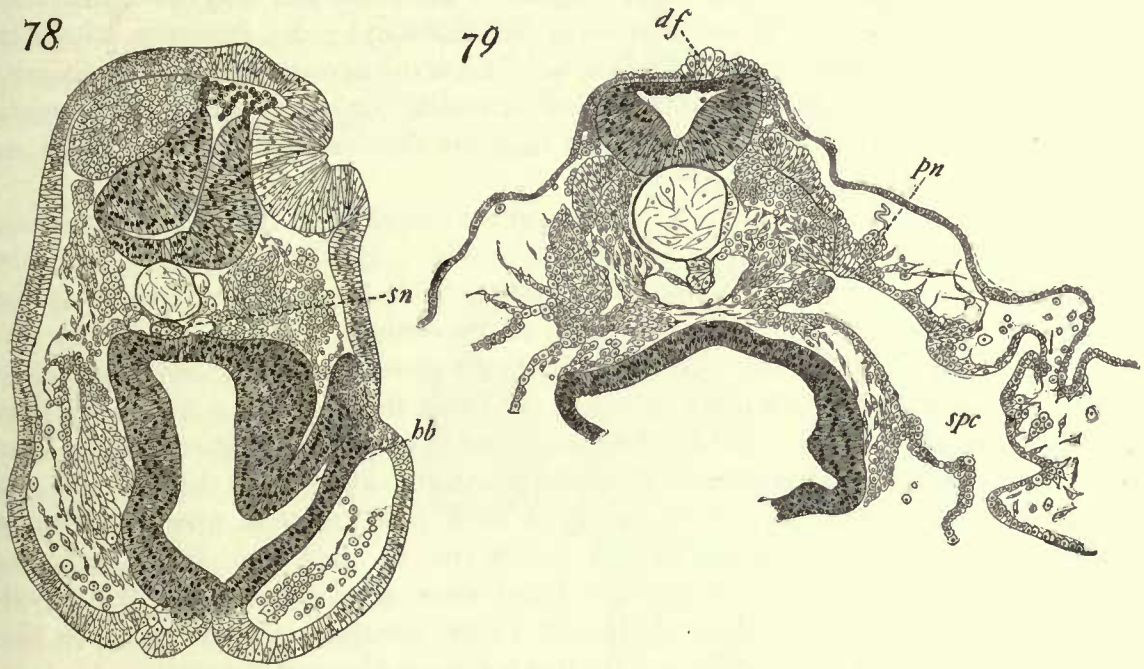


Fig. 78.—Transverse section passing through the posterior head region of embryo of plate VII, fig. 42. At the right the section traverses an auditory vesicle and the hyomandibular evaginatioo. The latter fuses with the ectoderm, which here invaginates, but no opening has as yet been formed.

Fig. 79.—Transverse section through the middle of the trunk region of the preceding embryo.

df. Ectodermal anlage of dorsal fin. *pn.* Pronephros. *spc.* Body cavity.
hb. Hyomandibular evagination. *sn.* Subnotochordal rod.

A third embryo of this stage is pictured in plate VIII, fig. 49[a] to [d]. It measured about 35 mm. in length, and was observed living. It was this embryo whose capsule was taken accidentally on a trawl line during one of the writer's visits at Pacific Grove. As already noted, it was found developing in a creamy fluid. When placed in a watch-glass, its general position and color were as here represented. It lay for a while on its side, its diminutive yolk-sac extending outward from the body and the delicate tail region showing constant undulatory movements. Most conspicuous were the bright-colored vessels on the yolk-sac, which outlined a vitelline circulation obviously shark-like. The visceral cavity showed red through the delicate wall, and in the gill region there were prominent bead-like dilatations, brilliant in color. One notes the bright red spot under the eye, which was later

found by sections to represent the spiracle.* Further details of the gill region are given in fig. 49[a].

In the various figures given of this embryo we note a number of advancing structures:

(1) The eyes are now well formed, protrude widely from the head, and are provided with a conspicuous lens.

(2) The region of the snout shows distinct modeling. Olfactory pits are present and are separate from the rim of the mouth. The snout region, it will be seen by reviewing the preceding figures, notably plate VII, figs. 44–46, does not correspond to the greatly dilated eminence which forms the cap-like knob surmounting the head. This appears rather in the region of the forebrain, and the writer does not, therefore, agree in the conclusions of Schauinsland (who, however, it will be borne in mind, examined Callorhynchus, not Chimæra) as to the fate of this singular organ. It has, we suggest, the function of providing for the growth of the contour of the antero-dorsal head region† rather than for the framework of the snout, as Schauinsland suggests.

(3) The mouth has broken through, and its margins are thickened. It shows distinct movements, although at irregular intervals, in the living young. Between the rim of the upper jaw and the eye appears the spiracle, and in a remarkably anterior position contrasted with that of an elasmobranch.

(4) The five gill-arches (plate VIII, fig. 49[d]) show well-developed lamellæ on their anterior margins, and from these are produced the external gills. The latter extend outward on either side to a distance equal to about the diameter of the head between the eyes. The presence of dilated spaces, blood-filled, in the external gills has already been recorded. It is worthy of note, perhaps, that when the present specimen was preserved masses of yolk (plate VIII, fig. 49[b]) were found adhering to the gill-filaments, a fact which may have some significance, since the blood-dilated spaces appeared at points adjacent to the attached yolk masses. In this stage, it may be added, the fifth gill-slit has not as yet broken through.

(5) The fins are well established. The lobe of the anterior dorsal fin, however, shows as yet no trace of a spine. The paired fins are distinct lateral folds, much as in the young shark; in fact, the pectorals are even precociously large. It may be added that the metameral elements of the fins were conspicuous in the living embryo, since blood-vessels were present and appeared in a series of brilliant spots. The ventral fins are drawn together immediately behind the anus, and no trace appears of a clasping organ or of a third pair of limbs.‡ The general arrangement of the fins is best seen in plate VIII, fig. 49.

(6) The yolk-sac, in spite of its small size, was perfect. Its structure is delicate, for at first its contour was smooth, but after the embryo had been kept living for several hours in sea-water, it was noticed that the surface of the sac

*This is not in the position in which Solger (Morph. JB., 1876, pp. 219–221) expected it to appear, *i. e.*, behind the articulation of the mandible.

†Possibly as a larval organ to protect the head when in contact with the wall of the egg-capsule.

‡ *Cf.* T. J. Parker, Nature, vol. XXXIX, p. 625. With regard to the non-appearance of mixipterygia, which certainly occur early in Chimæroid ontogeny (*cf. infra*, plate IX, fig. 50f, also text), it is possible, of course, that the present embryo was a female.

loosened at several points, giving the wavy contour noted in the figure of the entire embryo. The arrangement of the vessels is clearly shown, and one traces the posterior umbilical veins and the anterior vitelline arteries. At first sight the yolk-sac seemed to be attached anteriorly throughout the length of the heart region. Later examination, however, showed that a single stalk, albeit a very short one, connected the sac with the trunk in a fashion very much as in the young shark. (*Cf.* plate VIII, fig. 49[b]).

(7) The lateral line system of organs is already established. At either side of the eye sensory pits are present and the backward growth of the lateral line could be traced as far as the anal region.

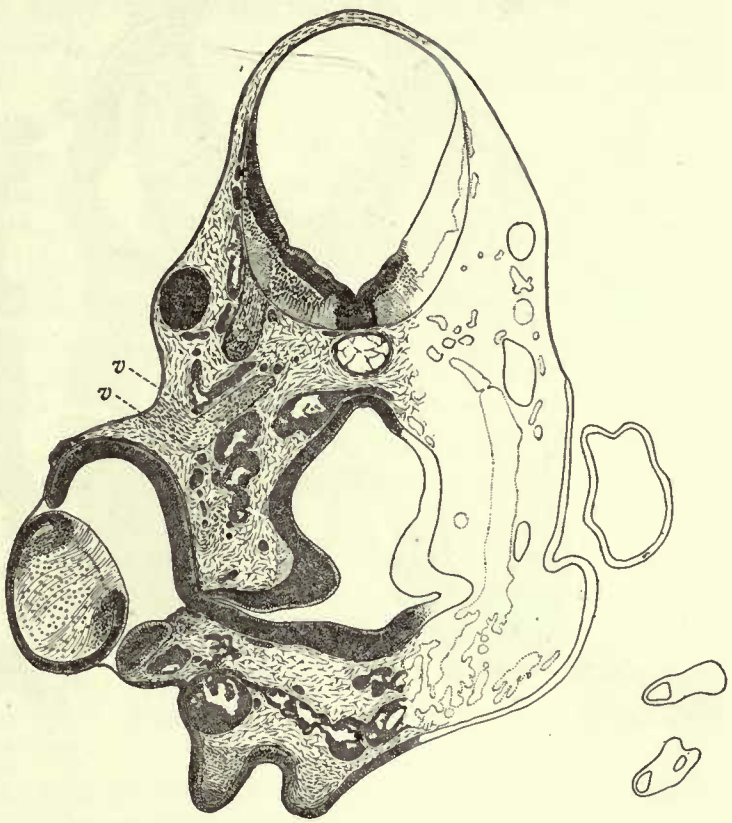


Fig. 80.—Transverse section through the eye region of the embryo shown in plate VIII, fig. 49.

v, *v*, Branches of anterior internal carotid.

DETAILS OF THE FOREGOING EMBRYO.

In the sections, figs. 80–83, are shown details of the foregoing embryo. In the first of these (fig. 80), in the eye structures one observes the proportionally enormous size of the lens. Particularly noticeable, also, are the elaborately branching vessels lying between the eye and the mid-brain (*v*, *v*), a symptom again of the embryo's precocious growth. In the following section (fig. 81) the spiracle (*s*) is seen to be continuous. Sections through an external gill-filament show, even more conspicuously than in shark, the presence of both vein and artery (*a*, *v*). In the same section we observe one of the blood-filled dilatations (*d*), which have already been commented upon. This appears at or near the end of the gill-filament.

In fig. 82, a section through the pelvic region just anterior to the anus, we observe on the right side the opening of a segmental duct at *sd*. Beside it, at *mt*, appears a mesonephric tubule. On the opposite side of the body a corresponding tubule, *mt*, opens directly into the body cavity. One observes in the same section a dilated caudal vein at *cv*, and above it the caudal artery. In the section, fig. 83, we observe that the unpaired fins are already well established and that they are made up largely of mesoblast. The caudal vein and artery appear as before, and the section traverses numerous muscle plates.

The latest embryo in the writer's material, one of the specimens secured by Professor Wilbur, measured 51 mm. in length. Its age was said to be six months. (Plate IX, figs. 50 and 50[a] to [g].) It is decidedly like the adult Chimæra, as can be seen from the figures; it has well-established snout (in which sensory grooves and pits appear), paired and unpaired fins, and clasping organs, showing that the present specimen was a male. On the other hand, two prominent embryonic characters still appear, viz, the yolk-sac (which in the present specimen is preserved only in part) and the external gills, a tuft of which is seen protruding from below the opercular folds. The external gills are shown in plate IX, fig. 50[a], [c], [e], and [g]. Their degree of differentiation is indicated in fig. 50[g], in which we note that in each filament one of the component vessels is less contorted than its neighbor, the filament thus presenting a crinkly appearance when viewed under a low power. Occasionally a terminal dilatation is seen. It will be noted that some of the filaments attain great length, although in general they are fewer in this than in the earlier stage, a process of reduction having set in at certain points.* In lateral view this embryo shows fragments of yolk attached to its side and to its paired fins, a condition probably artifact, although deserving mention, since in the younger stage yolk masses were observed attached to the gills. Before making the present sketch, a portion of the opercular fold and the neighboring external filaments were removed. The sensory canals are well indicated; that of the lateral line has now passed down the side of the body and has entered the tail region. The mandible is well established. In plate IX, fig. 50[c], we observe the extent to which the opercular folds overlap the tuft of external filaments; we here observe also that the frontal clasping organ

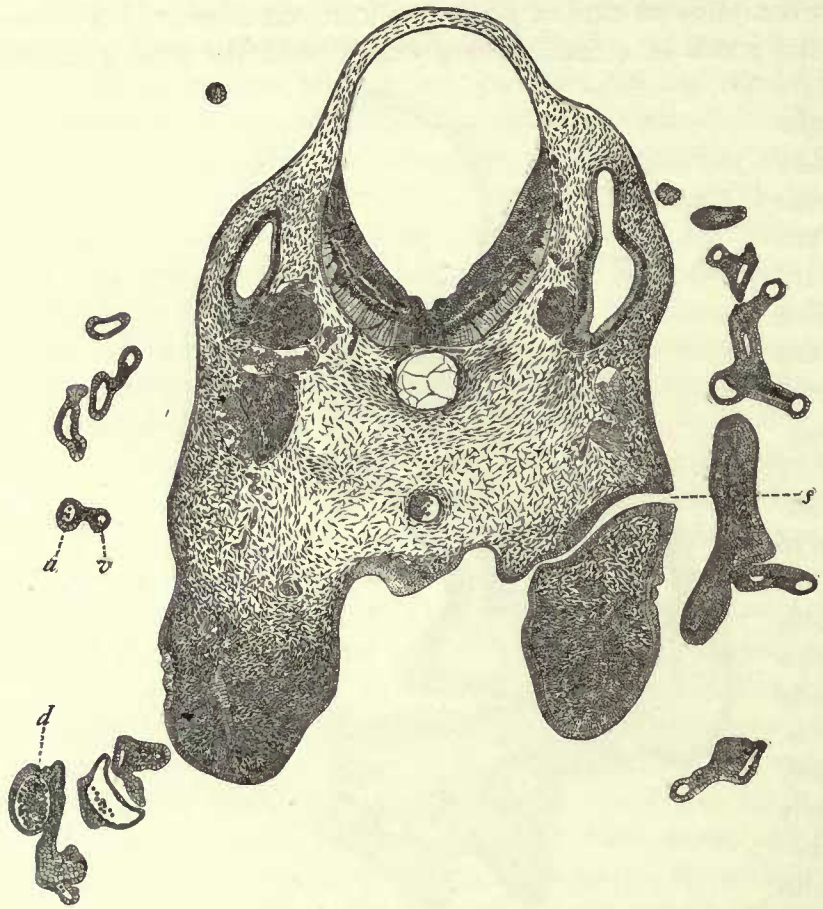


Fig. 81.—Transverse section passing through the otic vesicles of preceding embryo. At the sides external gills are shown.

a, artery; *d*, dilated blood knot in external gill; *s*, spiracle; *v*, vein.

Cf. also Schauinsland (*op. cit.*, Taf. XVI).

is long, narrow, and relatively of great size, suggesting its origin from an anterior fin spine, and interesting in connection with paleontological data (*cf.* figs. 132–137). In fig. 50[d], an idea is had of the extent of the overgrowth of the opercular fold on the ventral side of the head, and here is shown also that the external gill-filaments arise only from the anterior wall of the gill-slit, and that the external filaments increase in length as they pass toward the middle of each flap. A detail of the ventral fin is shown in fig. 50[f]. Here the mixipterygium is but a further differentiation of the base of the ventral fin (*cf.* plate VIII, fig. 49[b]), and the anterior clasping organ (*acl*) evidently represents the fin's anterior segmental elements (radialia) (*cf.* also fig. 112). The mouth region in this stage is noteworthy, since it shows that not only are the anterior and posterior dental plates (*adp* and *pdp*) present, but also a series of other eminences which are best interpreted as rudimentary dental plates. Similar structures are now described in detail in the work of Schauinsland on Callorhynchus (*v. infra*). The present figure also indicates the early stages in the curious lip cartilages of the Chimæroid. They arise at the sides of the mouth and suggest at this stage the corresponding structures in shark. In view of the recent work of Schauinsland and of the younger Fürbringer (Morph. JB., 1903, vol. XXXI, pp. 360–445), we recognize with interest the unpaired element at the mandibular symphysis which is held to represent the homologue of the basihyal of the hyoid arch. (*Cf.* fig. 111.) In commenting further upon this stage we note that in the eye the iris is well established, and that in the umbilical sac the yolk material is arranged in conspicuously concentric lamellæ (plate IX, fig. 50[d]).

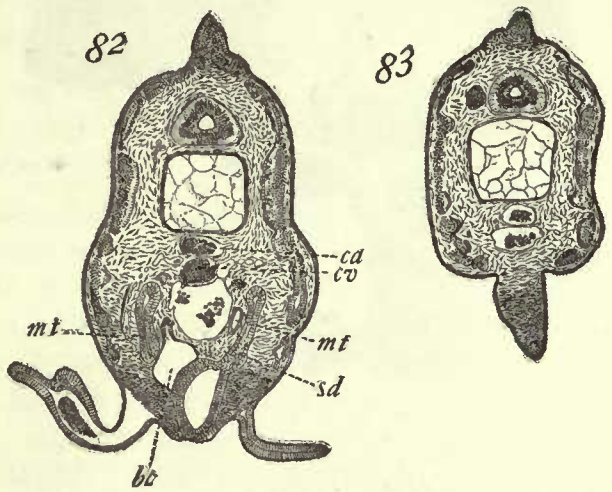


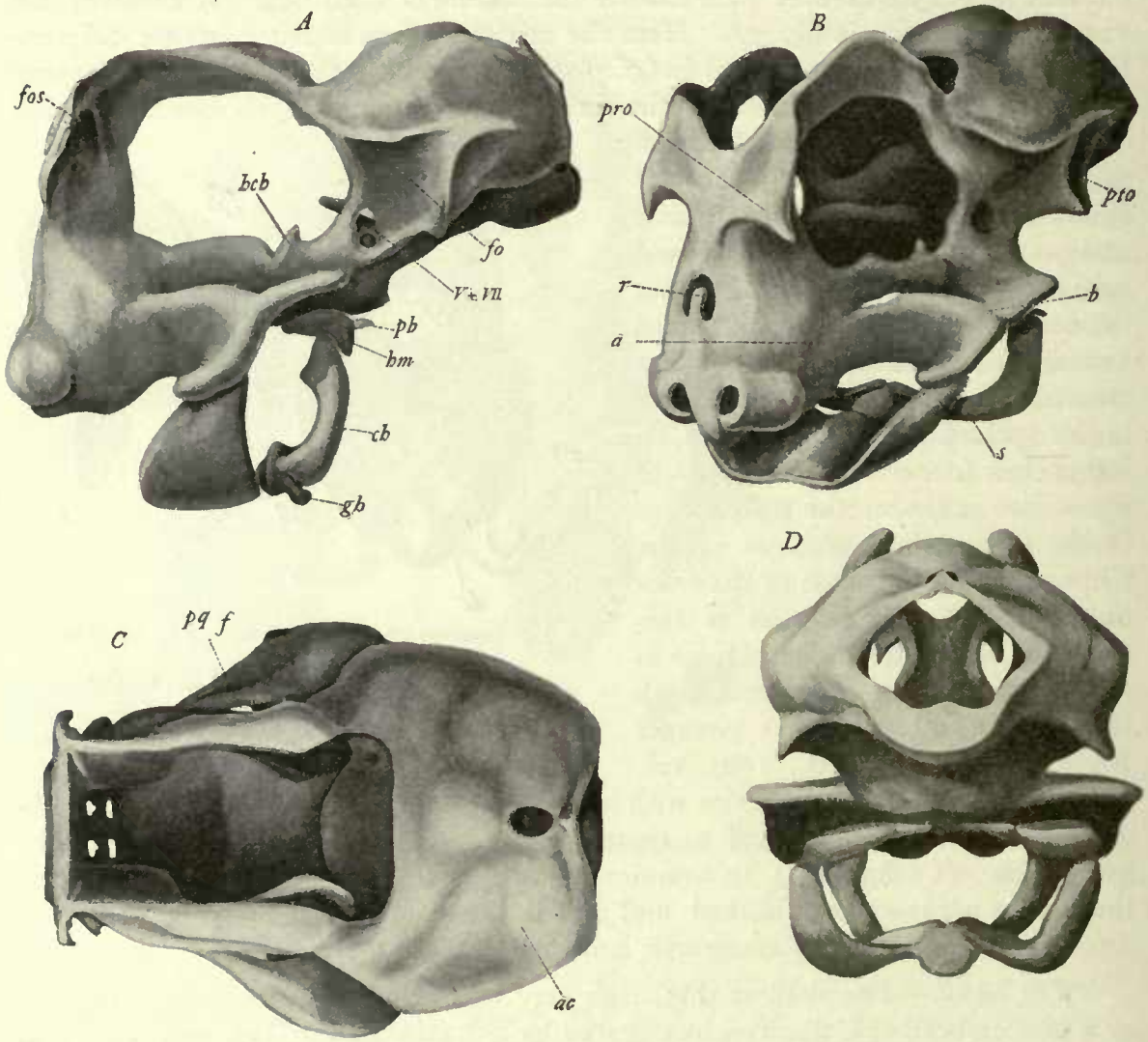
Fig. 82.—Transverse section through the region of the ventral fins of preceding embryo.

bc, Body cavity; *ca*, caudal artery; *cv*, caudal vein; *mt*, tubule of mesonephros; *sd*, posterior portion of segmental duct.

Fig. 83.—Transverse section through the tail region of the preceding embryo.

The Skull.—The skull at this stage may be compared instructively with that of a late embryo of Callorhynchus figured by Schauinsland in Taf. XVII, figs. 124, 125, 126, *op. cit.* The present figs. 84 A–D were, like the figures mentioned, prepared from wax-plate models. The embryo referred to by Schauinsland is more advanced than the present one, although the difference in age does not appear to be conspicuous. On the other hand, the figures of a younger Callorhynchus shown in Schauinsland's Taf. XVIII, figs. 130 and 131, can not be compared satisfactorily with the present specimen of Chimæra, for its skull was evidently far less mature, a large part of the model having been based upon outlines of procartilage. A study of the foregoing figures indicates that the skull of Chimæra is, at a corresponding growth period, the more highly modified; the orbits are larger, the snout

region is wider and more compressed, the palato-quadrate is reduced and transferred to a more anterior position, nor is it as distinct an element as Schauinsland figures it in the kindred genus. As further evidence of the more modified character of the skull of Chimæra, we observe that the preorbital ridges are curiously flattened, forming together a transverse brow-plate in the young skull; and that the



Figs. 84 A–D.—Reconstruction of skull of Chimæra embryo shown in plate IX, fig. 50. The model is shown in lateral, three-quarters dorsal, and caudal aspects.

a–b, Anterior and posterior points at which the palato-quadrate element has fused with the cranium; *ac*, roof of auditory capsule; *ch*, ceratohyal; *fo*, foramen through which the ophthalmic nerve passes out of the cranium; *fos*, foramen through which passes the superficial branch of the ophthalmic nerve; *gh*, basihyal; *hch*, hypochordal portion of the basis cranii; *hm*, hyomandibular; *pb*, pharyngobranchial; *pqf*, palato-quadrate fissure; *pro*, preorbital process; *pto*, postorbital process; *r*, median rostral cartilage; *s*, spiracular cleft later retained as the foramen through which the hyomandibular branch of the seventh nerve passes to the under side of the skull; *V+VII*, foramen for fifth and seventh nerves.

postorbital ridges are reduced in size. We note also the greater width of the cranium in Chimæra and the lesser development of cartilage in the region between the orbits. In short, we can justly conclude that at corresponding stages the skull of Callorhynchus more closely resembles that of a young shark than does the skull of a young Chimæra. The proportions in the case of Callorhynchus are distinctly

shark-like, so also are its early rostral cartilages. In Chimæra, on the other hand, the developmental processes, evidently abbreviated, produce larger orbits, larger auditory organs (from this is due the broadening of the skull noted above), coalescence of foramina, and altogether a more mature modeling of the head.* In this form, moreover, we find in the hyoid arch more perfectly developed ceratohyal and greatly reduced pharyngobranchial elements. It follows, I conclude, in view of these and other evident specializations,† that one can not reverse the order of comparison and regard Chimæra as resembling the more closely the ancestral type from which in turn Callorhynchus and sharks developed.

COMPARISONS WITH OTHER CHIMÆROIDS.

Before concluding the account of the later embryonic stages of Chimæroid, which we have hitherto based upon *C. colliei*, reference should be made to the conditions known in other genera and species.

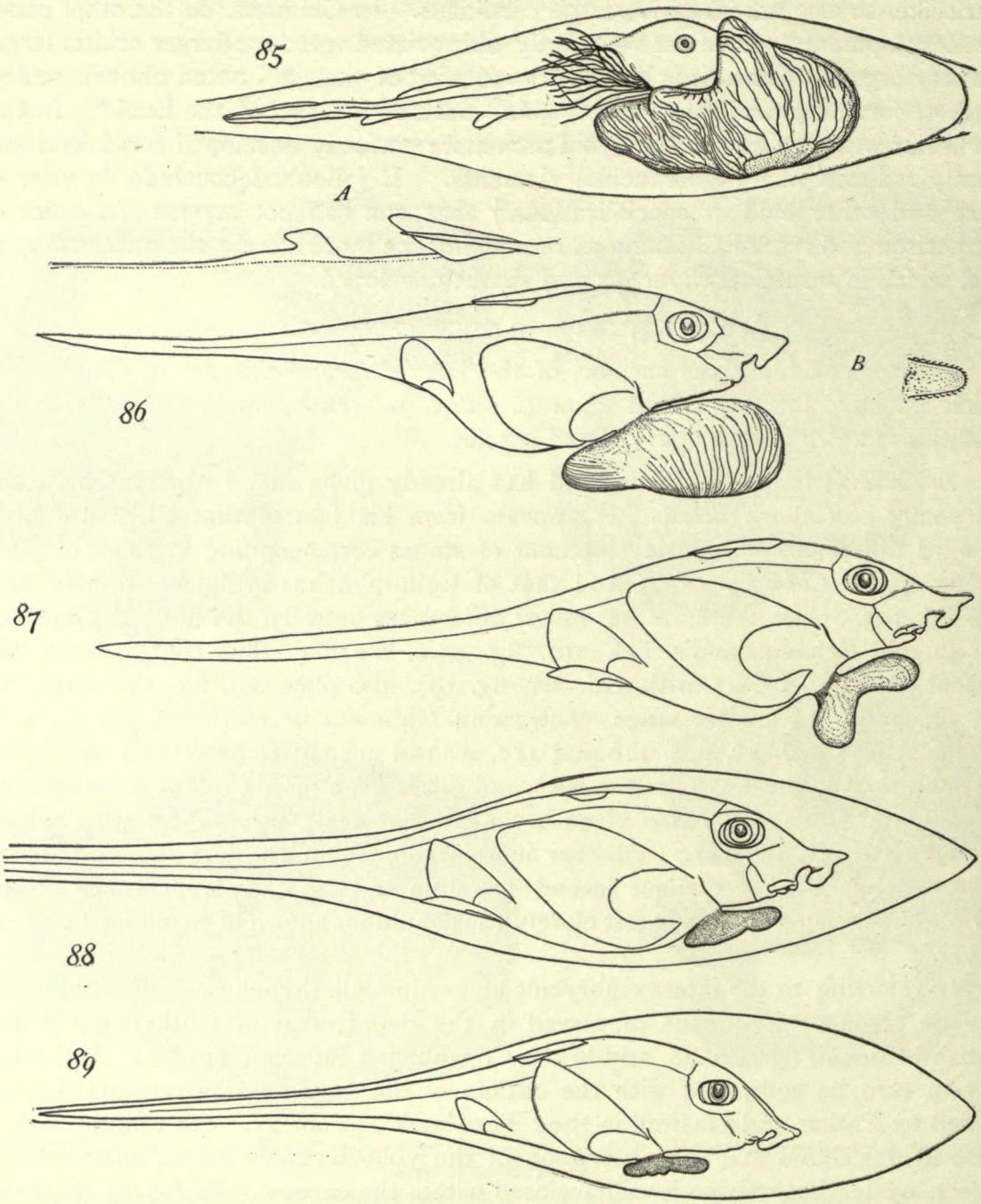
In Callorhynchus.—Schauinsland has already given many observations upon the young of Callorhynchus. It appears from his figures that there are little outward differences in the development of stages corresponding to those of plate VII, fig. 45, of *Chimæra colliei*, and that of Callorhynchus in Schauinsland's Taf. XIII, fig. 105. Also there are but minor differences between the present plate VII, fig. 42, and Schauinsland's Taf. XIII, fig. 98. We may thus compare also the present plate VII, fig. 45, with Taf. XIV, fig. 107, also plate VII, fig. 43[a], with Taf. XIV, fig. 106. In a later stage, contrasting Chimæra in plate VIII, fig. 49, with Schauinsland's Taf. XV, figs. 116 and 117, we can not fail to note the more shark-like conditions in the Australian species, and this is even more evident if we contrast the still later stage of *C. colliei* given in the present plate IX, fig. 50, with Schauinsland's Taf. XV, fig. 121. Observe in this connection the less tapering tail of Callorhynchus, a more distinct second dorsal fin and the early appearance of the row of dorsal scales which suggest closely the conditions shown in Scyllium by Paul Meyer.

In referring to the latest embryonic stages in Callorhynchus, outline drawings may be given of specimens preserved in the department of ichthyology in the British Museum, figs. 86–88, and in the Copenhagen Museum, fig. 89.‡ And these may in turn be compared with the outline of the young Callorhynchus, fig. 85, figured by Parker and Haswell in their Text-book of Zoology. An examination of these figures shows that the absorption of the yolk-sac takes place, as one would expect, while the embryo is still inclosed within the capsule. In fig. 85 the yolk-sac is of irregular shape, rather large, and the embryo still retains its external gills. In figure 86 the sac, still large, is somewhat bilobed, a condition which becomes

Cf. also in this connection the more advanced condition of the mixipterygia in Chimæra (plate IX, fig. 50f, and Schauinsland's Taf. XVI, fig. 120).

†In morphological regards *cf.* the reduction of dermal defenses, great size of head, reduction of caudal region, differentiation of dorsal fin, specialization of clasping organs, modification of brain.

‡For the privilege of examining these valuable specimens the writer is indebted to Mr. Boulenger and to Dr. Winge.



Figs. 85–89.—Latest stages in the development of Callorhynchus within the capsule. Nearly actual size.

85. Callorhynchus "antarcticus." Detail of figure given by Parker and Haswell.

86. Callorhynchus sp. Stage in which the yolk-sac is reduced in size.
A, Outline of dorsal fin when unfolded. B, Detail of frontal clasping organ with surrounding row of dermal denticles.

87 and 88. Callorhynchus sp. Late stages in absorption of yolk-sac. The foregoing three figures are after specimens in the British Museum. (Cf. p. 34.)

89. Callorhynchus "antarcticus," showing very late stage in the absorption of the yolk-sac. After sketch of specimen from New Brighton, New Zealand, preserved in the Zoological Museum at Copenhagen.

intensified in the later stage, fig. 87. In fig. 88 the sac is still irregularly bilobed and in figure 89, where it has been almost completely taken into the embryo, the anterior lobe is still present. Observe in connection with these figures that the shape of the sac is obviously correlated with the shape of the embryo inclosed within the capsule.* A further consideration of these figures leads us to conclude that in the latest stages of development the embryo of Callorhynchus rests on its side, and in this position the dorsal fin is observed to lie neatly tucked against the side of the body, the dermal web of the fin being folded under the depressed spine. So also the paired and unpaired fins are closely apposed to the sides of the body, the continuous dorsal and anal fins folding closely around the side. The dorsal fin folds over the trunk towards the left side of the embryo. An outline of its margin, slightly raised, is shown in fig. 86 A. In this stage the appearance of the frontal clasping spine is indicated in fig. 86 B. This corresponds obviously to the condition which is figured in a younger stage by Schauinsland in his Taf. XVI, fig. 122.

In Chimæra.—The only late embryonic stage known to the writer is the one preserved in the Jardin des Plantes and figured by Professor Vaillant in his "Travailleur" report (1882), a specimen which the writer had the opportunity of examining through the courtesy of its describer. This specimen (fig. 90 A, B), probably of *C. affinis*, was dredged in the Bay of Biscay, together with fragments of its egg-capsule. A small yolk-sac is adherent; this is of spherical form, and appears to have been delicately connected with the body of the embryo. It is possible, of course, that the present spherical form of the yolk-sac may have been the result of the specimen having been freed from the capsule, for under this condition the yolk-sac would probably have assumed its present shape. It may be noted that the surface of the sac was deeply creased with blood-vessels, somewhat as indicated in fig. 90 A. Noteworthy in this specimen is the great length of the hinder trunk (and tail) which, it will be seen, is proportionately longer than in *Chimæra colliei*, and much longer than in Callorhynchus, and it is also to be mentioned that the long urostyle shows that the continuous dorsal fin could not have extended functionally into this posterior region. Clasping organs are developed, and, as shown in fig. 90 B, they attain even now a considerable size, about one-third their adult (proportional) length. This condition is noteworthy as indicating again a precocious type of development, sexual characters having been differentiated, although the embryo is small in size and provided with a considerable yolk-sac.

IMMATURE YOUNG.

Four stages of "larvæ" of *Chimæra colliei* are shown in plates X and XI, to illustrate especially changes in outward form, proportions, and coloration. The specimens figured in plate X were secured by the *Albatross* during its work on the Pacific coast, and were kindly placed at the writer's disposal by the United States National Museum. The youngest specimen figured (fig. 51 and figs. 51[a] and [b]) was evidently lately hatched. It still shows the scar marking the point of intrusion

*The irregular outline of the yolk-sac would, by analogy, probably be filled out if the living embryo were removed from the constricting capsule.

of the yolk-sac (plate x, fig. 51[b], *ys*); its form at this stage is probably modeled somewhat differently from that of the latest stage of the encapsuled embryo; thus the membranes of the unpaired fin in the tail region are probably less marked than in the earlier stage (comparing the embryo of plate ix, fig. 50) in which this membrane serves as an organ for carrying out the water used in the respiration of the

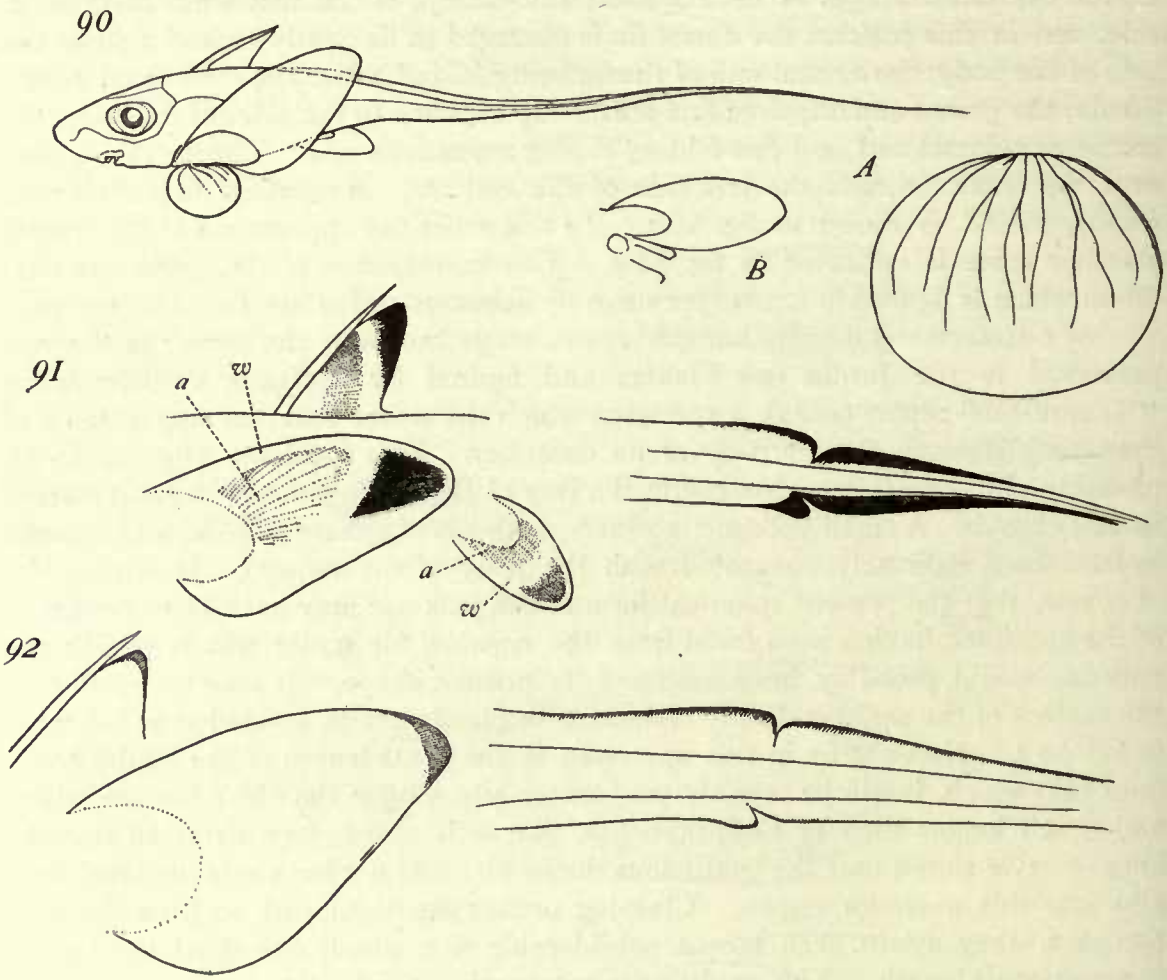


Fig. 90.—Late stage of Chimæra affinis (?).

The yolk-sac is largely resorbed. The present is the type specimen of Professor Vaillant, and is preserved in the ichthyological museum of the Jardin des Plantes, bearing the number 42392. In spite of its small size (its total length is only about 11 cm.) it shows a well-developed mixipterygium (B). A detail showing the vascular supply of the yolk-sac is indicated at A.

Fig. 91.—Detail of early Chimæra monstrosa, showing larval coloration.

After sketch of specimen in the museum of Tromsoe. Colors are indicated, *a*, ashen, *w*, white.

Fig. 92.—Detail of Chimæra monstrosa indicating final larval coloration. After sketch of specimen in the museum in Copenhagen.

encapsuled young. The advancing characters of the earlier young may best be followed by contrasting figs. 51, 52, and 53. The changes thus observed are:

In proportions.—The head length of the embryo, measured for example anterior to the base of the dorsal fin, decreases as we ascend the scale; in the earlier stage it measures about 20 per cent. of the entire length, in the latest about 16 per cent.; the eye alters little in size, but the region of the head lying below the eye increases notably; the shape of the pectoral fin changes progressively; almost as wide as high in the first figure, it becomes nearly twice as high as wide in the latest stage. So,

too, the unpaired fins change proportions notably; in the stage shown in plate x, fig. 52, their width is much greater proportionately than at other stages.

In shape.—The shape of the trunk undergoes noteworthy changes. In the stage shown in plate x, fig. 53, it is much longer proportionately than in the earlier and later stages. We note also that the dorsal fin (or rather that portion of it posterior to the first dorsal) changes from continuous to lobate and then again later to a lower and less lobate form, during progressive development.

In color.—Pigmentation appears progressively. In the youngest stage the pigmented areas are dorsal. In the stage of plate x, fig. 53, pigmentation is more marked on the sides of the body than at any other stage. The sharpness in the coloration of the distal margin of the dorsal fins is most conspicuous in the stage of plate x, fig. 52; also a distinct larval coloration is noticed in the pectoral fin, a well-marked color being present along the anterior margin of this fin and in the anterior portion of its dermal web. Observe also the distinct patch of pigment at the base of the dermal web in plate x, fig. 53. Noteworthy, further, is the progressive increase in the number of pigmentless blotches; few in fig. 51[a], they become numerous in fig. 53[a], and small and most numerous in the stage of plate x, fig. 54. Similar changes in coloration affect the region of the eye.

A late stage in the development of *Chimæra colliei* may finally be referred to in plate xi. At this age the young fish has attained nearly mature size (*i. e.*, about three-quarters of that of the adult), although it is still distinctly "larval." Its coloration is darker (*cf.* fig. 1), making the small pigmentless spots more conspicuous. The margins of the fins, on the other hand, are pigmented, and with these we may contrast the fin margins in the adult, figs. 1 and 2, especially in the latter figure, where we observe that the anterior rim of the paired fins, notably the ventral, are pigmentless. We observe also distinct changes in proportions from the earlier stages; the length of the fish anterior to the anal region is now scarcely more than one-half the total length; in the earlier stage figured it is less than one-third. In the present specimen, a young male, the ventral fins partly uncover the mixipterygia; the ventrals are small in size, surprisingly so when we consider the length of the entire fish. At this growth period the young of this species occur in schools and sometimes appear in shallow water.*

In other species similar changes in colors and proportions are probably present in "larval" young. In one species, *Chimæra monstrosa*, they are present in even a more marked condition. In a young specimen preserved in the museum of Tromsoe, to which the writer's attention was kindly called by Dr. V. Storm, the coloration was brilliantly marked. Although not larger than the specimen shown in plate x, fig. 53, it had developed dorsals sharply marked with black, pectorals with an ashen blotch and with a white anterior rim, a pattern which has been reproduced from a sketch in the present fig. 91. It is evident, moreover, that in *C. monstrosa* this stage is of brief duration; for in a second and equally well-

*The present specimen was taken, together with 22 others, in a water depth of less than 10 feet, near Port Washington, Puget Sound, June, 1896, in a single haul of a herring seine. In this locality Chimæra is rarely taken in shallow seines. The specimens measured from 30 to 40 cm.

preserved specimen of this species—one which was examined in the Copenhagen collection—the colors had notably changed. The pigmented margins of caudal and postdorsal fins had become reduced to a dusky band, and the marking of the pectoral was limited to a mere fuscous blotch at the fin tip (fig. 92). The length of this specimen was but about two inches greater than the former one.

From the foregoing notes we may justly conclude that Chimæra undergoes a series of "larval" changes. That these are adaptive remains still to be proven, a verdict which, it may be remarked, applies equally well to many if not all the "larval" changes of teleosts, but the fact that such changes do occur in the hatched young is noteworthy in its bearing on the specialized nature of Chimæroid development. It is also, I believe, significant that the "larval" coloration of the young of *Chimæra monstrosa* occurs at an earlier relative period than in *C. colliei* (*i. e.*, that the distinctness of coloration, which in *C. colliei*—a smaller species by the way—is shown in a specimen twelve inches in length, is attained in *monstrosa* by the time the young measures but about seven inches), for this denotes that the structures of *monstrosa* are the more highly differentiated and that this species is of later origin. In another direction it contributes testimony as to the abbreviation of developmental processes.

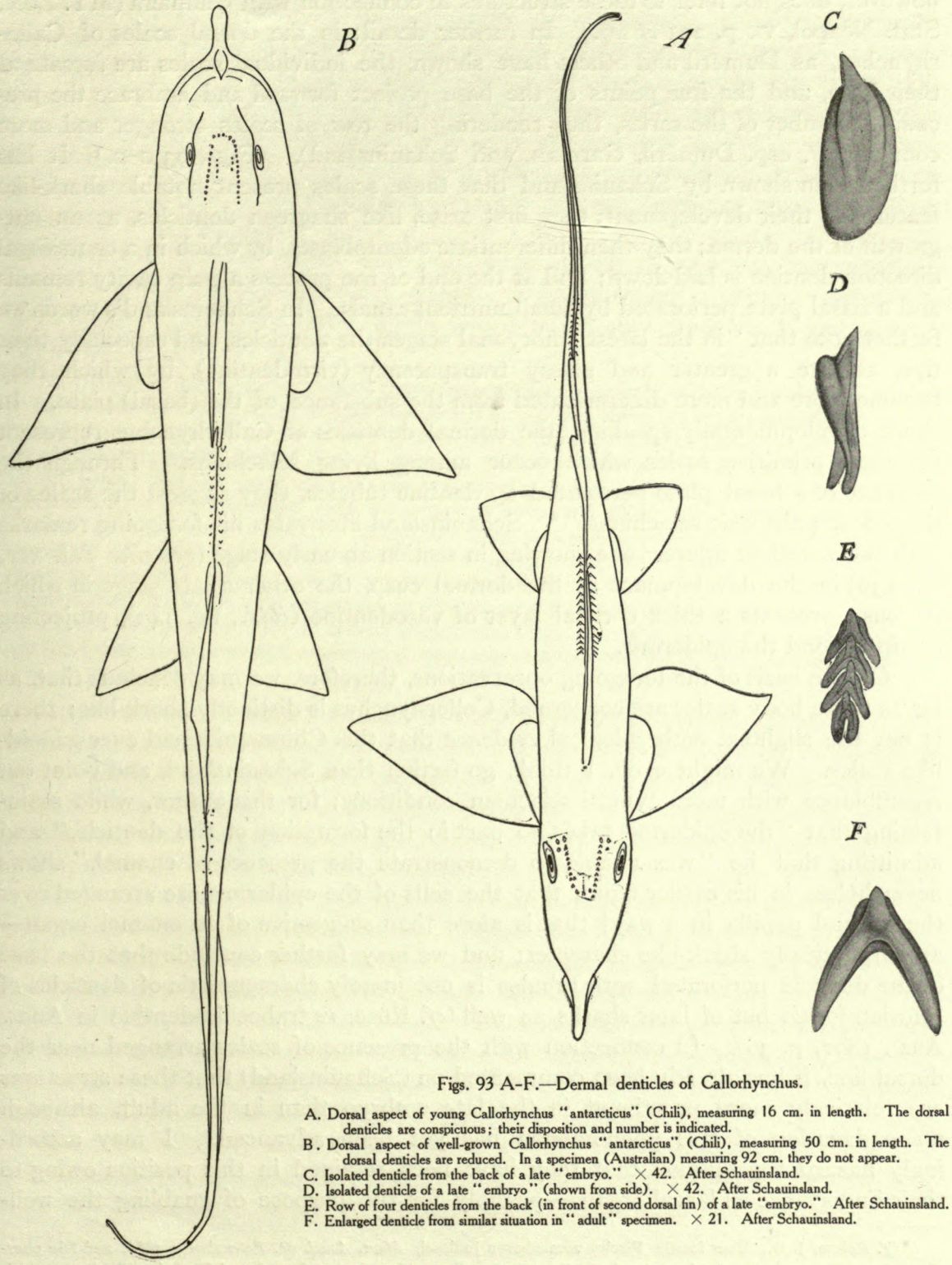
ORGANOGENY.

INTEGUMENT AND DENTITION.

In the major problem of the position of Chimæroids the evidence of scales and dentition claims an important place. For the question has been raised repeatedly whether the dentition of these fishes is fundamentally different from that of sharks, and whether the characteristic tritoral plates may not have retained primitive gnathostomal characters (Jaekel). And it has similarly been queried (Pollard) whether the present integumental defenses of Chimæroids may not prove the rudiments of a complete body armoring. We may accordingly review at this point the evidence in the matter of integument and teeth afforded by a study of the recent forms, both in adult and in embryonic condition.

It has long been known that recent Chimæroids retain shagreen-like structures. These occur in greater or less number (*a*) on either side of the median dorsal line; (*b*) in connection with sensory canals, especially in the suborbital region; and (*c*) in the male as organs of retention *in copulo*.

(*a*) Shagreen-like scales on either side of the median line are most numerous in Callorhynchus, where they form rows, each including about a dozen scales, in three definite tracts, *i. e.*, in the head, between the first and second dorsals, and between the second dorsal and the caudal fin (figs. 93 A and B). In Harriotta they are smaller and less numerous. In Rhinochimæra they are tumid and uncalcified, occurring along the fleshy anterior margin of the caudal fin, obsolescent elsewhere. In Chimæra they are rudimentary or absent. These scales occur, therefore, in a regressive series, at one end of which stands Callorhynchus, at the other Chimæra; and it is significant, I believe, that a condition closely similar to Callorhynchus occurs in sharks, *e. g.*, Pristiurus and Scyllium, as figured by Paul Meyer, who,



Figs. 93 A-F.—Dermal denticles of Callorhynchus.

A. Dorsal aspect of young Callorhynchus "antarcticus" (Chili), measuring 16 cm. in length. The dorsal denticles are conspicuous; their disposition and number is indicated.
B. Dorsal aspect of well-grown Callorhynchus "antarcticus" (Chili), measuring 50 cm. in length. The dorsal denticles are reduced. In a specimen (Australian) measuring 92 cm. they do not appear.
C. Isolated denticle from the back of a late "embryo." × 42. After Schauinsland.
D. Isolated denticle of a late "embryo" (shown from side). × 42. After Schauinsland.
E. Row of four denticles from the back (in front of second dorsal fin) of a late "embryo." After Schauinsland.
F. Enlarged denticle from similar situation in "adult" specimen. × 21. After Schauinsland.

however, does not refer to these structures in connection with Chimæra (MT. Zool. Stat. Neapel, VI, p. 221 *et seq.*). In further detail: in the dorsal scales of Callorhynchus, as Duméril and others have shown, the individual scales are furcate at their base, and the free points of the base project forward and embrace the preceding member of the series, thus rendering the row of scales stronger and more compact (*cf.* esp. Duméril, Garman, and Schauinsland). (Figs. 93 C–E.) It has further been shown by Schauinsland that these scales present notable shark-like features in their development; they first arise, like shagreen denticles, as an outgrowth of the derma; they then differentiate odontoblasts, by which in a centrifugal direction dentine is laid down; and at the end of the process a pulp cavity remains and a basal plate perforated by small nutrient canals. In Schauinsland's words we further note that "in the latest embryonal stages the denticles, and especially their tips, acquire a greater and glassy transparency (vitrodentine), by which they become more and more differentiated from the substance of the (basal) plate. In short, developmentally speaking, the dermal denticles of Callorhynchus represent the most primitive scales which occur among living selachians. Through the presence of a basal plate perforated by dentine tubules, they suggest the scales of the oldest palæozoic selachians."* Schauinsland illustrates his foregoing remarks with two excellent figures, one showing in section an early stage (*op. cit.*, Taf. XIX, fig. 139) in the development of the dermal cusp, the other a late stage in which the cusp presents a thick cortical layer of vasodentine (*ibid.*, fig. 140), projecting its tip beyond the epidermis.

On the basis of the foregoing observations, therefore, we may conclude that, as far as these body scales are concerned, Callorhynchus is distinctly shark-like; there is not the slightest embryological evidence that this Chimæroid had ever ganoid-like scales. We might even, I think, go farther than Schauinsland, and point out resemblance with more typical selachian conditions; for this author, while maintaining that "the epidermis takes no part in the formation of the denticle," and admitting that he "was unable to demonstrate the presence of enamel," shows nevertheless in his earlier figure that the cells of the epidermis are arranged over the dermal papilla in a way† that is more than suggestive of an enamel organ—an emphatically shark-like character; and we may further conclude that the base of the denticle perforated with tubules is not merely characteristic of denticles of Silurian forms but of later sharks as well (*cf.* Röse, *re* trabeculo-dentine in Anat. Anz., 1897, p. 36). In connection with the presence of scales arranged near the dorsal line, it has already been commented on (Schauinsland) that these structures are relatively more prominent in the late embryo than in the adult, although no explanation of this phenomenon has yet been advanced. I may accordingly hazard the opinion that they have been retained in this position owing to their importance as larval organs—possibly for the purpose of enabling the well-

Cf. Rohon, J. O., Über fossile Fische vom oberen Jenissei, *Mem. Acad. St. Petersburg*, 1889, and Die obersilurischen Fische von Oesel, *Mem. Acad. St. Petersburg*, 1893. He refers to denticles of Thelodus-like forms which the recent researches of Traquair have associated with fishes which are in some regards shark-like.

†*Cf. e. g.*, Jentsch, B., Beitr. z. Entwick. u. Struktur d. Selachierzähne. Leip. 1897, fig. 6.

developed young to maintain its position in the egg-capsule, possibly also for the purpose of protecting the delicate dorsal fin, *i. e.*, by keeping it from rubbing against the walls and the roof of the capsule, during the movements of the young fish. According to this view the dorsal scales of the young Callorhynchus after the time of hatching are to be looked upon merely as rudimentary organs.* And it may be pointed out, in this connection, that when these enlarged dorsal scales are developed in shark embryos they appear *only in those forms in which development takes place in egg-capsules.*†

(*b*) Small dermal plates have long been known to occur in Chimæroids in connection with the sensory-canal system. Pollard makes a special reference to those situated in the suborbital canals, and Schauinsland gives the following notes upon them (*op. cit.*, p. 13):

> In the immediate neighborhood of the mucous canals—I have investigated those only situated on the head—there also occur dermal calcifications. I find there (in transverse section) in the floor of the canal (in the neighborhood of the skull) a large plate, and in addition at its sides and bounding it four to six conical caps of dentine. The development of these is like that of the denticles, save that the plate contains no pulp cavity, while the lateral small hard structures present such a cavity, if indeed only in a narrow form, and filled with few cells, whereby they come to resemble a small denticle. These calcifications are also probably only the rudiments of former dermal denticles which came to sink down at the same time that the epidermis was invaginated to form the mucous canals; in this process they lost their primitive form and underwent degeneration. In adult, and especially in a number of fossil Holocephali the slime canals are surrounded by a great number of closely compressed rings formed of calcified and bony material; these had their origin through a process of pressing together the single dentine-like bony caps noted in the embryo.

In the matter, then, of the character of these plates in living forms, we may again conclude that they are equally derived from solitary dermal denticles, shark-like in type. There is no evidence, on the side of embryology at least, that these plates result from a breaking down of larger structures. It is only necessary to note further that these structures in Callorhynchus are most marked in their likeness to the selachian condition, and that they are least marked in the case of Chimæra.‡

(*c*) In all recent Chimæroids numerous denticles are present in the male, *i. e.*, on the frontal clasping organ, on the mixipterygium, and on the anterior pelvic clasping organ. These denticles have a transparent, almost glassy character. In the frontal clasping organ of Callorhynchus, they occur not only at the tip of the organ itself, but also proximalward and at the front and sides of the depression into which this clasping organ fits; but in the other genera, the denticles are limited only to the tip of this organ. It follows, accordingly, that in Callorhynchus appears again a more shark-like character, *i. e.*, a greater number of denticles spread over a larger extent both of the clasping organ itself, and of the sheath into which the

*In a specimen of *Callorhynchus* "*antarcticus*" (Australia), measuring 92 cm. in length, the dorsal denticles have disappeared.

†The tubercles in the encapsuled Scyllium (de Philippi, Paul Meyer) may well have a similar function. By Paul Meyer they are described (*op. cit.*, p. 224) as rudimentary organs, viz., the remains of the ancestral annelidan parapods!

‡As to the condition of these dermal elements in fossil Chimæroids, *v.* figs. 138 and 139; by evidence thus obtained the conclusion becomes definite, *i. e.*, that the shagreen of recent forms has been greatly reduced from a condition altogether shark-like.

clasping organ is usually depressed. In this connection we call to mind the great size of the clasping organ in the young Callorhynchus, suggesting its origin from an anterior fin spine (*cf.* figs. 132–137); its small size in Chimæra on the other hand indicates the later derivation of this genus.

This induction is also supported by a study of the clasping organs connected with the ventral fins in the antero-pelvic clasping organ of Callorhynchus. We observe that this structure is furnished with many dermal denticles—40 or thereabouts in the case of *Callorhynchus antarcticus*, according to Duméril, whereas in the various species of Chimæra and in Rhinochimæra the number is reduced, varying usually from about six to three.

In the mixipterygium shagreen denticles occur plentifully. In the case of one arm of this trifid organ in *Chimæra colliei* the denticles extend proximally as far as the base of the organ. In the other two arms the shagreen is limited to tracts near the tips. An abundant supply of these denticles is, however, present, representing, in fact, tracts of shagreen. In *Chimæra monstrosa*, on the other hand, the amount of the shagreen is less, a condition which furnishes another reason for regarding this species as the more modified. In *Rhinochimæra pacifica*, as the writer has already noted (Jour. Sci. Coll. Tokyo, vol. XIX, p. 10), the shagreen at the tip of the mixipterygium is greatly reduced. In Callorhynchus, on the other hand, it is as abundant as in the case of *Chimæra colliei*.

DENTAL PLATES.

These have always been the stumbling-block in comparing Chimæroid with sharks, for by only superficial comparison have the tritoral areas in the dental plates of Chimæroids been regarded as equivalent to the teeth or clusters of teeth in the shark. Nor has paleontology as yet been able to elucidate the problem, even to the degree in which it has thrown light upon the origin of the dental plates in the lung-fishes. In fact, as we shall later note, the study of the dentition of fossil Chimæroids leads us at the present time to no decisive results. The development of the dental plates might therefore be looked to to furnish evidence as to the nature of these structures. For it is well known that through embryology a flood of light has been thrown upon the mode of origin of the dentition of lung fishes. Accordingly, we conclude that one of the most important sections of Schauinsland's memoir on Callorhynchus is devoted to the question of the mode of origin of the dental plates.

Schauinsland's account, indeed, is of such value in the present connection that I have been led to quote it in freely translated form (*op. cit.*, pp. 13–16):

In even their earliest stages the dental plates are laid down as distinct elements, *i. e.*, four above and two below, and there is at no time a definite indication that these are composed of simpler elements which have fused together. The upper anterior plates are certainly simple; the remaining pairs, however, show along their hinder (caudal) border a somewhat trifid arrangement. In this region, too, the plates with their three ridges pass into a fold of the skin, and here their growth takes place. (No trace appears even in earlier stages of the median (unpaired) mandibular tooth which has been described in fossil Chimæroids.) If we regard the three ridges as rows of teeth which have become fused together, they would have obviously a certain similarity to the dental plates of dipnoi or even of teleosts (*e. g.*, Anarrhichas); and we

might accordingly regard the anterior plates as premaxillary or vomerine, although in the latter regard, *i. e.*, *re* premaxillary and vomerine elements, we query whether we can justly introduce this comparison in the holocephali. On the other hand, if the comparison be a legitimate one, we might even go farther and regard the more median ridge of the large plates of the mouth-roof as equivalent to the fused vomerine teeth, and look upon the remainder of these plates as having arisen from fusion of the elements in a double row of palatine teeth. Of course, however, such an interpretation would be purely hypothetical.

One is inclined to look upon the anlage of a dental plate as the product of a single and enormously enlarged dental papilla, circumscribed by a dermal fold, the induplicature of which is deepest at the posterior margin of the papilla. The first deposition of hard material begins at the outer surface of the papilla, and takes the form of a thin cap of dentine, soon, however, the tooth-substance appears below at the points where the plate is to come in contact with the cartilage of the head. And almost at the same time trabeculæ and lamellæ appear between, *i. e.*, in the substance of the plate, and produce a meshwork of spongy tooth-substance (pulp-dentine). The mode of origin of the plate resembles closely that of bone when derived from connective tissue (*e. g.*, in Sphenodon). The mesenchyme cells in the papilla are collected together closely at certain points and become transformed into odontoblasts, and from these, peripherally, the dentine takes its origin. It may be remarked that the dentine is sometimes laid down in an irregular way, with branching processes, its canals ramifying, unlike the parallel canals of true dentine. Occasionally trabecules of the dental mass, especially in older individuals, show a somewhat lamellar structure, and those which are first differentiated, that is, those lying innermost, are distinguishable from the later lamellæ by their capacity to become stained. As already noted, the entire dental plate is finally formed of a meshwork of dentine-like material, whose trabecules thicken with age, so that finally the plate attains a high degree of hardness. The spaces between the meshwork represent collectively a large, greatly branched pulp cavity, whose cells in part have retained their former reticular arrangement, in part have become odontoblasts, as far at least as they become opposed to the trabecules. In the various ramifications of the pulp cavity blood-vessels are often present. Enamel is not deposited; nevertheless the epidermis cells must have a certain influence on the character of the dentine, since the dentine becomes glassy in character when in contact with the epidermis, but remains unchanged whenever the epidermis is lacking. The dental plates are fastened to the head cartilage by means of a firm layer of connective tissue, which indeed here and there may enter the substance of the plate, and for still stronger attachment claw-like outgrowths arise from the base of the plate, especially from its anterior and lateral portions.

Finally, I must refer to the presence of remarkable structures in the dental plates, which occur only within the ridges above referred to. These take the form of a chalky mass, which appears in cleared preparations and can be traced throughout the entire length of a dental ridge; it is partly inclosed within the meshes of the trabecules of the dentine, and by these partly again broken up into rounded masses and processes. In transverse section this chalky mass presents the appearance of a section of a many-rooted tooth, while in longitudinal section its substance appears continuous, although greatly fenestrated. A more detailed examination shows that we are here dealing with an especial variety of dentine; that is, differentiated from odontoblast-like embryonic cells, whose processes grow deeply down and develop canals which from their parallel arrangement recall strikingly those of typical dentine. In any event, the material in question can more accurately be designated as dentine than can the remaining spongy substance of the dental plate. From the latter it is also distinguished in remaining colorless after treatment with the usual stains for bone, and especially in retaining permanently, even in the grown Callorhynchus, its soft and uncalcified condition. It may be noted that this soft dentine is not present in the youngest embryonic stages; it appears shortly after the caudal ends of the plate are established and extends gradually from a hindward into a more anterior position.

It has nothing to do with the origin of the hard structures of the plate, since it appears after these have been laid down. It usually appears somewhat deeper than the outer surface of the plate; later it often comes to lie in close contact with it, and even extends thence inward, not infrequently coming to be associated with the remaining meshwork of the dentine. What the significance of this structure is remains in any event doubtful, and only with reserve do I express the opinion that these soft masses of dentine represent the rudiments of former rows of single or

already fused teeth, which had primitively passed from behind and taken up a position on the dental ridges. In the case of these teeth (a similar process occurs in the ontogeny of Ceratodus) spongy dentine, or bone-like masses, were differentiated in the course of phylogenetic development, and these became finally of greater value for purposes of nutrition than the separate teeth; and they accordingly fused together, overgrew the teeth, and in the end completely enveloped them. And since the teeth had no longer their primitive function, they came to lose their limy structure and degenerated, remaining in the condition in which we see them to-day. While their arrangement in three rows possibly indicates an alliance with the higher forms, their mode of successional growth suggests the origin of the rows of teeth of selachians.

The results of the foregoing observations of Schauinsland, it will be seen, are disappointing to those who on *a priori* grounds anticipated that the dental plates of Chimæroids would in the ontogeny of recent species be found to be formed of the coalesced bases of separate tooth elements, which, in their turn, would of course be homologous with those of sharks. One may, nevertheless, I believe, take a somewhat more hopeful view of this problem, in view of the evidence above provided. In the first place, however, in order that there may be a better understanding of the terms of the problem, it will be found expedient to review briefly the characters of dentition known among the more prominent types of recent Chimæroids, for there is room for the belief that Callorhynchus, in spite of its many archaic features, may prove to have modified the conditions of its dental plates, or at least parts of them (the "tritors"), more completely than some of the other forms.

To this end we may compare the dental characters of Harriotta with those of Rhinochimæra, as representing extreme types in Chimæroid dentition. In fig. 94 A are shown in Harriotta the dental plates and the roof of the mouth; in fig. 94 B the dental plates, tongue region and floor of the mouth, and, in figs. 94 C and 94 D, corresponding regions are shown in Rhinochimæra. Contrasting these forms, we notice that in Harriotta the dental plates are studded with peg-like eminences, some of which, both in the upper and in the lower "jaws," form together tumid tracts or ridges. These peg-like eminences, "tritors," are found to pass deep into the substance of the dental plate; thus, where the plate is flattened and more or less transparent, as at the anterior margin, the peg-like structures are seen to pass backward, forming long and narrow cores. These are evidently of hard, bony texture, for they often stand out from the plate-like ridges when the intervening basal portion of the plate is worn away. We also observe that the adjacent mucous membrane of the roof, sides, and floor of the mouth is studded with distinct papillæ. These, it will be seen, correspond to the "tritors," in size, prominence, and closeness in arrangement, and may, I believe, from the evidence of similar structures in the mouth region of various fishes, be looked upon as homologous with tooth-forming papillæ.* It will thus be observed, as in figs. 94 A, 94 B, that they occur within the stomadeal region; they are absent in the dorsal wall of the pharynx; they are present, however, on the floor of the mouth, and are

*In a recently published paper on the oral and pharyngeal denticles of elasmobranchs (Proc. Zool. Soc., 1905, I, pp. 41–49), Imms gives reasons for homologizing similar structures in sharks with teeth. He did not, however, find the papillæ present in the specimen of *Chimæra monstrosa* which he examined.

continued along the floor and sides of the pharynx. In Rhinochimæra, on the other hand, the dental plates have become thin and have developed hard cutting edges, giving the mouth an almost beak-like appearance. In the plates tritoral areas are reduced to thread-like elements, so delicate that they become difficult to

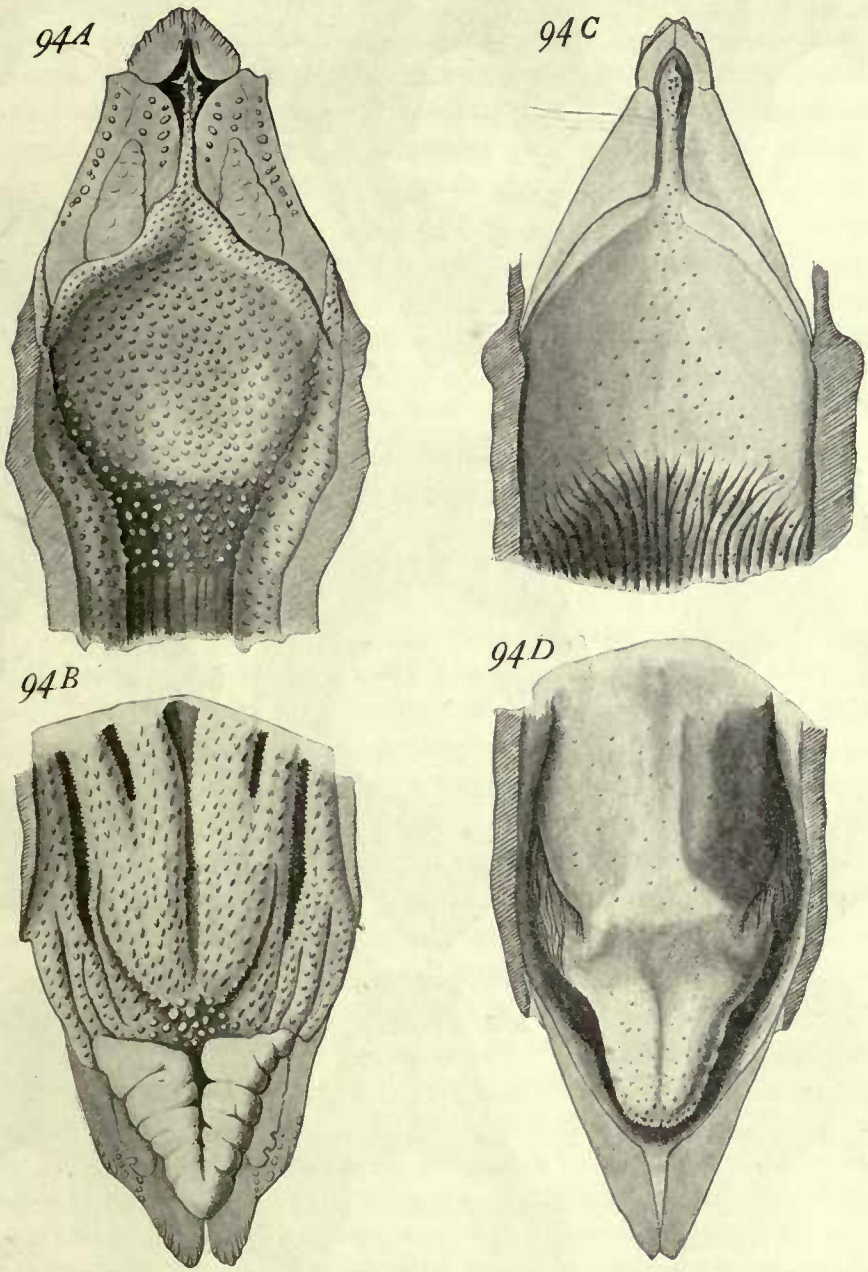
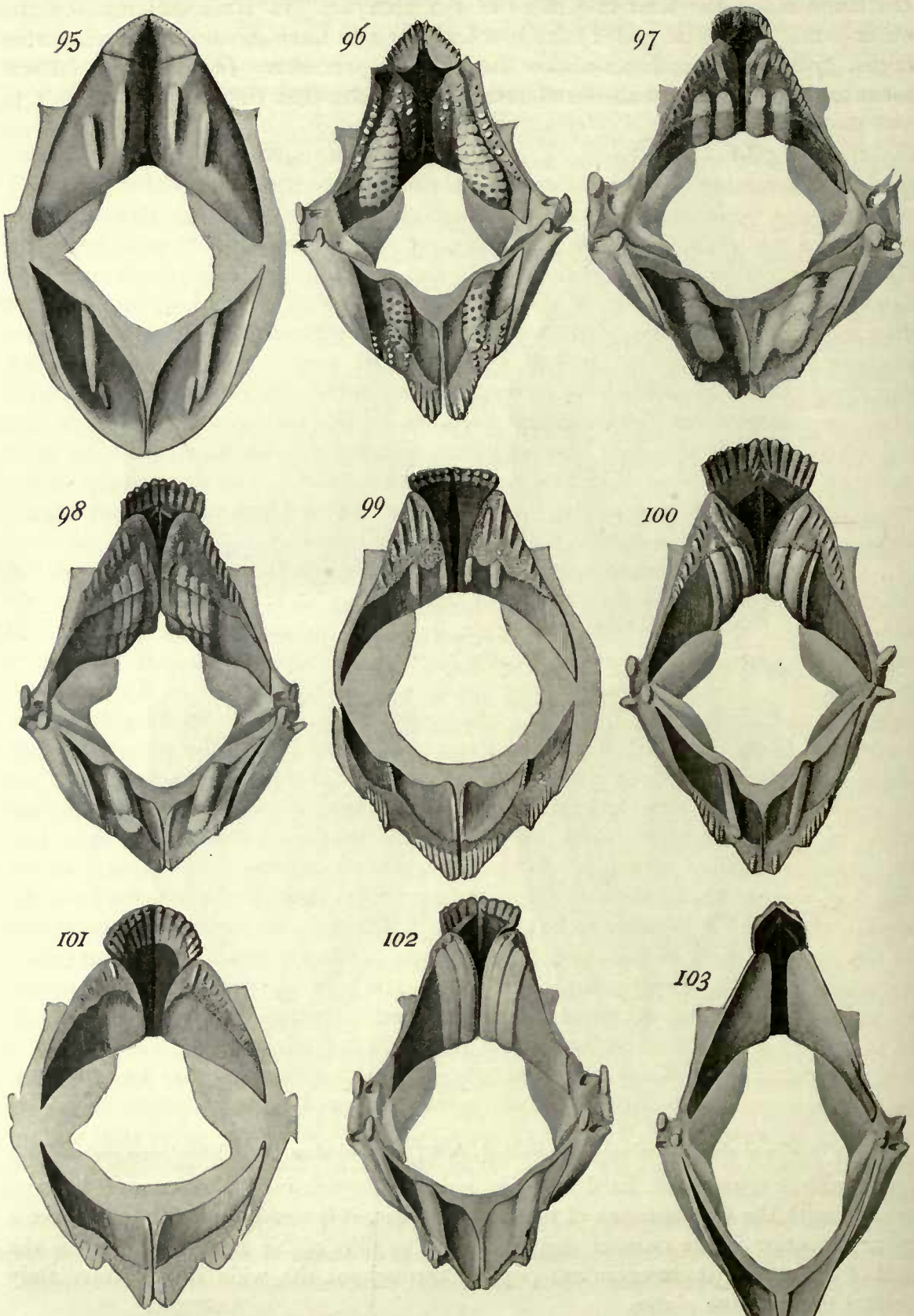


Fig. 94.—Dental plates, and roof and floor of mouth of: A, B, Harriotta raleighana. C, D, Rhinochimæra pacifica.

distinguish even in the hard anterior pair of "vomerine" plates; and in connection with the obsolescence of the tritoral areas, it is now interesting to observe a great reduction in the number and size of the papillæ of the mouth. Thus on the roof of the mouth there occur no papillæ throughout the wide tract immediately behind the palatine plates.



Figs. 95 to 103.—Dental plates of Chimæroids.

Fig. 95, Callorhynchus "callorhynchus"; 96, Harriotta raleighana; 97, Chimæra phantasma; 98, C. mediterranea; 99, C. monstrosa; 100, C. mitsukurii; 101, C. affinis; 102, C. colliei; 103, Rhinochimæra pacifica.

Comparing now a series of the dental plates of Chimæroids (figs. 95 to 103), we may first place side by side those of Callorhynchus and Harriotta (figs. 95, 96). It then becomes clear, I think, that the ridges in the dental plates of the former genus correspond to the clustered tubercles in Harriotta, a comparison which is well borne out by the embryological studies of Schauinsland, for it will be recalled that the separate ridges of Callorhynchus were shown to consist of a mass of chalky centers in which the lamellæ of dentine were parallel to one another, although their substance, as was noted, remains uncalcified (*cf.* fig. 105). A similar state of affairs, it may be remarked, occurs in the posterior part of the large tumid ridges in Harriotta, for these ridges and their tritors can be readily sectioned. On the other hand, the anterior eminences of the same tumid ridges are found to be much harder than the neighboring bony plate, and may with less question, therefore, be regarded as representing true teeth. Indeed, it is, after all, a matter of minor importance that these tritoral elements have never hardened in the case of Callorhynchus; for when we consider the thickness and hardness of the surrounding bony plate, we are led to conclude that this may well have usurped the function of the separate denticles, and that these therefore remain undeveloped. The same rudimentary condition is probably true of the minute tritoral points which one finds along the anterior margin of the vomerine plates in Callorhynchus.

Continuing the comparison, one can with fair definiteness understand the relations between the dental plates of such forms as Harriotta and *Chimæra phantasma*. For, in the latter, the wide tritors at the base of the palatine and mandibular plates (fig. 97) are evidently homologous with the clustered tubercles in Harriotta. In *C. phantasma*, however, the crushing surfaces of the plate are smoother and less extended. In *C. mediterranea* (fig. 98) the dental plates have become more oblique (slanting) in their manner of attachment, the posterior flange of the plates intruding deeply below the mucous fold in the roof of the mouth. In *C. monstrosa* (fig. 99) the tritoral areas of the palatine plates are less numerous, while in the mandibular plates they are more abundant, but show less clearly the peculiar banded structure of the foregoing specimen. In *C. mitsukurii* (fig. 100) the conditions are not widely different from those in the species from the Mediterranean. A peculiar arching appears in the palatine plates, and the ridges on the posterior face of the mandibular plates, although smaller, are more conspicuous. In *C. affinis* (fig. 101) the proximal tritoral areas were not observed, and altogether the grinding margin of the palatine and mandibular plates was narrower. In *C. colliei* (fig. 102), while the tritoral ridges on the posterior faces of the palatine and mandibular plates are (usually) conspicuous, the grinding edges of these plates are exceedingly narrow. And in *Rhinochimæra pacifica* (fig. 103), finally, we attain a condition, as we have already noted, in which the tritoral areas are reduced to obsolescence, the entire distal margin of the plate functioning as a cutting edge.

From what has already been said regarding the dental plates in *C. colliei* (p. 19), I think we may safely conclude that a wide range of variation occurs in the dental plates of Chimæroids. Thus the tritoral structures may vary in number, size,

and arrangement; in fact, one might even go so far as to maintain that from a large series of dental plates of one species of Chimæra one might obtain variants which, separately considered, would be placed with other species. Moreover, from the function of these crushing plates, it is not unnatural that marked differences should appear in specimens of different ages and from different localities (*e. g.*, from those individuals which have lived upon different food material). In short, we incline to the belief that changes in the dental plates of Chimæroids do not predicate as wide divergences in lines of descent as one would naturally expect. From the standpoint of adaptation, furthermore, admitting the extreme value of physiological adaptation in dental plates within the limits of the present group, we obtain a suggestion why phylogenetic changes are not recapitulated favorably in their development. In a form, for example, like Callorhynchus, in which the basal (trabecular) portion of the plates has become greatly developed in the adult, we naturally expect that there will be less opportunity—shall we say time?—for the tritors to recur in development in a separate and finished form. If they do appear, they appear regularly only in "family" or in "generic" form, soon to be remodeled or erased. Thus we find in Callorhynchus, according to the figures of Schauinsland, that these tritors do occur in later embryonic stages (fig. 105), although this author does not refer distinctly to the relation of dermal cusps to tritors in Chimæroid plates. Following briefly the problem of the dentition of Chimæroids, we may again refer to the presence of numerous papillæ in the mouth region of these forms. For, by analogies in other fishes, these structures may well represent rudiments of discrete denticles. It is, therefore, of particular interest that in the case of Callorhynchus, where the dental plates are heaviest and largest, we find a corresponding increase in the size of the papillæ. For it may be suggested that papillæ which have become calcified either singly or in groups, have retained their dentitional (and ancient) trend in evolution, while those which remain soft have survived because they have undergone a change of function. The similarity in dental and non-dental structures is shown strikingly in the roof of the mouth of Callorhynchus (fig. 104), after Schauinsland. That shown in the roof of the mouth of Chimæra (plate IX, fig. 50[e]), although not

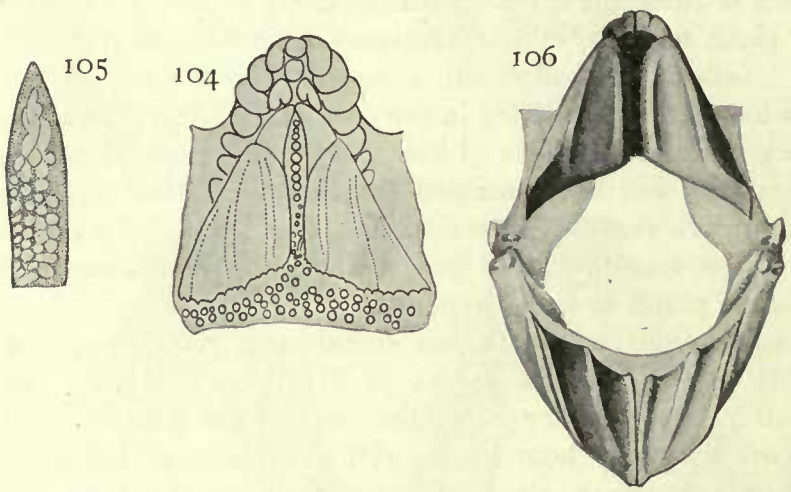


Fig. 104.—Callorhynchus callorhynchus. Dental plates and neighboring mouth parts of late embryo (about 110 mm. long). After Schauinsland.

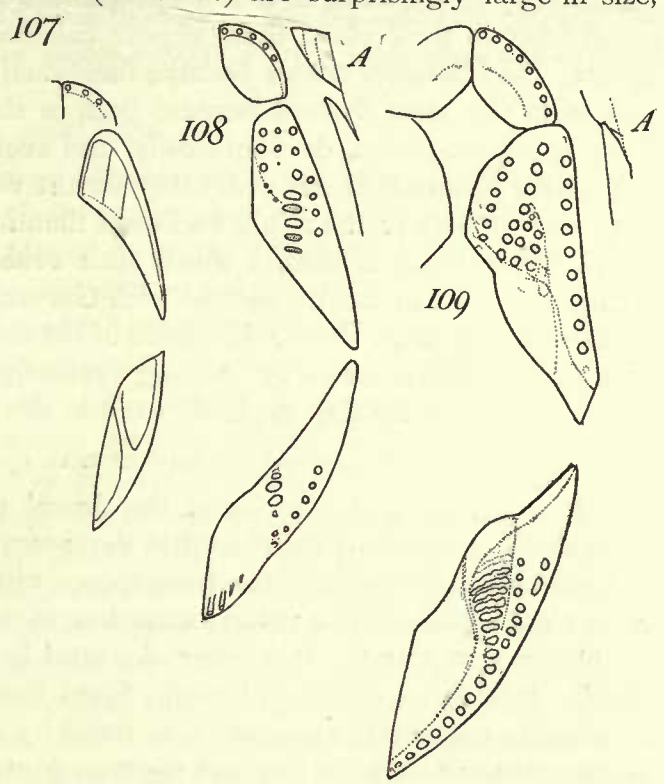
Fig. 105.—Callorhynchus. Detail of middle ridge of mandibular dental plate of specimen slightly younger (about 95 mm. in length) than the preceding. The dental ridge is seen as a transparent object. After Schauinsland.

Fig. 106.—Callorhynchus. Dental plates of "larva" measuring about 16 cm. After specimen in museum of Columbia University.

as conspicuous, is none the less suggestive when we compare it with the strictly tritoral conditions shown in Harriotta, fig. 94 A.

DENTAL PLATES OF LARVAL CHIMÆROIDS.

Furthermore, if one compares the dental plates in Chimæroids of different stages of growth, one is impressed with the evidence of larval adaptations. The plates of a Chimæroid recently hatched (*C. colliei*) are surprisingly large in size, but instead of spreading out in the form of crushing plates, they protrude marginally, forming relatively high edges and function evidently in cutting. Moreover, the substance of these juvenile plates is glassy (*cf.* Schauinsland, *re* vitrodentine) rather than horn-like or chalky, and their margins are sharp and brittle. It is clear, therefore, that the plates grow during earlier stages, notably at their outer or secant margins, and it is a probable conclusion that this condition of growth is correlated with the special feeding requirements of the young. In later stages the plates broaden and thicken, the secant edges become less and less conspicuous, and gradually the tritoral areas appear. The latter, at least in the species examined, are developed first vaguely, in extended tracts or ridges, and in these there later arise discrete eminences. This is the condition indicated above in Callorhynchus (*cf.* also with fig. 95 the juvenile plates shown in fig. 106); it is even more marked in *Chimæra colliei*, and it is to be observed in such a form as Harriotta. Of the last form we may introduce sketches of three stages of the dental plates.* In the first (fig. 107) the plates are frail, although well formed, and with secant prosilient edges; they have already ridges outlined and their clouded color (especially in the palatines) is probably due to the presence of vitrodentine. In the second stage (fig. 108) a number of distinct tritoral eminences appear. And in the final stage (fig. 109), the largest specimen of Harriotta recorded, the tritors are well differentiated.



Figs. 107–109.—Harriotta raleighana. Dental plates (somewhat diagrammatic) of three individuals measuring respectively 10, 49, and 64 cm. At A the lateral aspect of the vomerine and palatine plates is given.

*For the privilege of examining this unique material the writer is indebted to the United States National Museum. He wishes especially to express his thanks to its Assistant Secretary, Mr. Richard Rathbun, and to its assistant curator of Fishes, Mr. Barton A. Bean.

From the foregoing characters in "larval" dental plates, and they are certainly in the general line of Garman's observations,* we conclude that among the many specializations in the young Chimæroid may be included a larval dentition, *i. e.*, preceding the appearance of tritors. It may also be remarked that the tritors themselves, when they come to appear in the different forms of Chimæroids, occur in point of time in interesting sequence. In Callorhynchus they appear in the embryo (95 mm.), while it is still encapsuled, but they fail to develop into typical structures; in their place there appear calcified ridges representing collections of tritors. In Harriotta tritors become functional at a period shortly after hatching, and from this time onward increase both in size and number. In Chimæra they occur at a later period, develop slowly, and even in the adult are relatively few, and the plates themselves early develop secant margins. In Rhinochimæra, finally, they appear only in the adult, and even then in rudimentary form. In the Chimæroid series, there is thus, I think, such evidence of progression, even in recent forms, that we can hardly assume with Garman that from a condition like that in Rhinochimæra arose the dental plates of the other genera. On the contrary, in the case of Rhinochimæra we are dealing evidently with a terminal form, one in which the tritors fail to develop perfectly even in the adult.†

CONCLUSIONS CONCERNING THE DENTAL PLATES OF RECENT CHIMÆROIDS.

A comparison of a series of the dental plates of recent Chimæroids, as we have seen, strengthens the view that these structures are compound, *i. e.*, formed of separate denticle-like elements, homologous with the dental plates of certain sharks, *e. g.*, Cestracionts. The tritors, according to this view, represent dental eminences, simple or compound. But more doubtful is the homologue of the dental plate itself. It may represent either the fused bases of teeth like the Cestracionts, or a structure entirely *sui generis*, *i. e.*, fused by a hardening of the connective tissue accumulated around the bases of the true dental plates. According to the observations of Schauinsland the embryological facts support more or less distinctly the origin of the tritoral ridges from many tooth-like eminences dentinal in structure. On the other hand, the same evidence tends to regard the substance of the dental plate itself as independent of the tritors. An examination of the larval dentition of Chimæroids throws, I think, a side-light on the foregoing discrepancy, for it is found

*Garman, however, interprets these characters (Proc. New Eng. Zool. Club, 1901, vol. II, pp. 75-76) not as larvalisms, but as primitive; thus, according to him "the teeth of Rhinochimæra are of a much less differentiated form than those of any other of the recent genera of the group; that is, their later stages are more like the earlier, and presumably more like the teeth of primitive Chimæroids; they approach those of the extinct myriacanths and the very early conditions of the teeth of other living Chimæroids, Chimæra, Callorhynchus, and Harriotta. In advanced stages the teeth of Harriotta differ from those of Rhinochimæra in possessing several series of tritors which in superficial aspect resemble, in shapes and arrangement, certain crowns of placodont teeth. On the teeth of Rhinochimæra there are no tritors; the teeth of the very young of the other living genera are similar; this no doubt is a mutual resemblance to those of a common ancestor, an index to derivation. * * *" To this interpretation, on the other hand, there are two somewhat critical objections: (1) that in Rhinochimæra, as this author has later observed, there are present tritoral points, small, it is true, but tritors none the less; and (2) that his conception of the dental plates of fossil Chimæroids (*e. g.*, Myriacanth) is not valid, for whatever be the puzzles of the dental plates of fossil Chimæroids they have always tritoral areas.

†They may be expected to appear in a more perfect condition in very old individuals, somewhat as they develop in the late rather than in the young larvæ of Chimæra.

that the dental plates of the adult are attained only after a process of metamorphosis, during which the marginally high, delicate, glassy, and secant plates of the young are worn down and give rise to the adult dental plates, broad and thick, studded with tritors. Obviously, therefore, if we accept the view that a larval dentition is present, it is clear that the substance of the dental plate can better be regarded as a "precocious segregation" of the basal elements of teeth, *i. e.*, along the outer marginal rim of the plates, than as a new and independent accession to the materials of development. All will admit, however, that the requisite proof of this conclusion can be presented only by paleontology. On a later page the evidence in this regard is summarized.

SKELETON.

The vertebrate column of Chimæroids represents, according to Hasse (1879) a polyspondyly, which he regards as typifying the ancestral condition in sharks. The column of Callorhynchus was examined from the standpoint of embryology by Schauinsland, whose conclusions I summarize as follows:

That the early growth of the chordal sheath resembles that of many sharks, inasmuch as its substance is invaded gradually, and only at few points, by mesenchyme cells. That cartilage appears quite late in development. That in each segment (metamere) appear both neural and interneural plates, as well as corresponding (*i. e.*, double) hæmal arches, especially throughout a greater portion of the tail region. That these cartilaginous arches do not grow around with their bases the secondary chordal sheath; this is only overgrown by a stout sheath of connective tissue; the latter together with the arches on the one hand and the secondary chordal sheath on the other forms the secondary vertebræ, but the secondary chordal sheath is not divided into separate (primary) vertebræ—the segmentation of the column being indicated only through these parate arches.

Schauinsland, in brief, has been able to find no vertebral centra, in the sense in which they occur in other fishes; and my own studies upon Chimæra have been no more successful in this important quest. No centra are found in either early or late "larval" stages. Nor do they occur, as I suspected they might, after the fashion of gerontic structures, in very large individuals. At the most, in the latter case, there was a fusion of neural and hæmal arches occurring in the region near the occiput, but nothing which could be interpreted as definite centra. There is still, none the less, the possibility that some form of centra were represented in the ancestral Chimæroid, and that they were gradually lost in ontogeny; indeed, as we shall later note in the Jurassic Squaloraja and Myriacanthus, centra appear to have been present in the anterior region of the column (figs. 138 and 140 c), where in all recent Chimæroids, indeed, the most perfect neural and hæmal supports appear.

The development of the skull has already been illustrated in several stages of Callorhynchus by Schauinsland, and in a single late stage of Chimæra by the present writer. The results of their observations are briefly these: The chimæroid cranium, instead of developing as a uniform trough-like brain-case (shark), appears, even in early condition, in a wonderfully complete form; it incloses the hindbrain,

the forebrain, and the nasal region; and it early develops conspicuous ridges which evidently support and protect the eyes. And it is the latter organs, it may safely be said, which have played the most important part in modifying the growth of the cranium. For the orbital region is of enormous size, occupying no less than 50 per cent of the entire length of the cranium;* and, correlated with this, between and above the huge optic capsules, the growth of cartilaginous structures is retarded. It follows, accordingly, that while the posterior and anterior parts of the chondrocranium are well developed, its mid- or orbital region is largely unformed, and this is, I take it, the reason, the principal reason, that holocephaly has been developed, *to weld strongly together the anterior and posterior parts of the cranium where primitively the orbital walls came to be suppressed as the eyes increased in size.* Certain it is that the wide palato-quadrate elements extend like firm beams between the anterior and posterior moieties of the skull, and afford at the same time a support for the great optic capsules. And in this result appears a suggestion why the palato-quadrates appear so early and are so large in size; in fact, in no stage examined has it yet been found that these palatine elements are altogether separate from the cranium. In the earlier stages described (Callorhynchus) they are separate only for about half their length, and from the details of that stage it is even doubtful whether greater separateness ever occurs in the development of this element, earlier stages showing probably a prochondrial continuum—very much as one sees it in the prochondrium of the paired fins of sharks. The skull of the Chimæroid, in a word, is specialized even in early ontogeny; witness, among other regards, the enormous size of the posterior clinoid process, the huge fosse for the infundibulum, the exaggerated preorbital processes, the median frontal crest, and the interorbital vacuity.

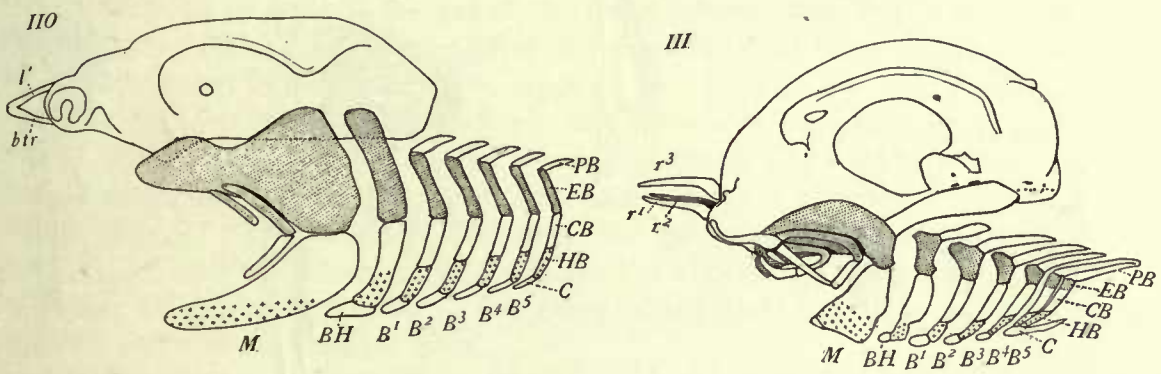
It is true, on the other hand, that certain skeletal structures in the chimæroid head retain a primitive character—possibly because they have been spared functional changes by the very fact that the palato-quadrate element has fused with the cranium. As primitive features we may here mention: (1) The perfect condition of the copulæ of the branchial arches. (2) The presence of a pharyngeal element in the hyoid arch which resembles the pharyngobranchials of the hinder arches. (3) The relatively large and discrete labial cartilages, as probable premandibular arches, and finally (4) the presence of a symphyseal cartilage as (Schauinsland, K. Fürbringer) the probable serial homologue of a basihyal. These characters are expressed, slightly schematized, in fig. 111, and may be compared with the corresponding structures in sharks (fig. 110). In these figures serially homologous parts are indicated by shaded or unshaded areas.

It should be mentioned, in passing, that even the branchial region of Chimæroid, in spite of the foregoing primitive characters, is not without convincing evidence of precocious specialization—witness the early appearance of the supporting extrabranchials of the hyoid arch, which are prophetic of the opercular flap of the adult.

The problem of rostral cartilages receives no evident solution in Chimæroid development. The anterior azygous process of selachians, which rises from the

* In the skull of the shark (*e. g.*, Scyllium) at a corresponding stage the orbit occupies about 30 per cent of the entire length of the cranium.

nasal septum (usually its base) is probably represented in the element which Schauinsland has figured as *sp* in his plate XVII, figs. 124, 126. However, in the Chimæroid the rostral supports (r^1 and r^2) later developed into long and separately jointed elements. Quite doubtful, on the other hand, are the homologues of the paired dorsal elements in the selachian rostrum, those figured, *e. g.*, by Kitchen Parker in Trans. Zool. Soc., vol. x, plate XXXVIII, fig. 1, as *btr*; they are possibly the homologues of Schauinsland's elements *s* in the figures quoted. Equally doubtful is the more dorsal azygous element (Schauinsland's r^3; *v.* the present fig. 111), which folds forward and becomes a main support of the produced snout in Callorhynchus; it certainly finds no homologue in sharks, and in view of the history of the frontal clasping organ in Chimæroids (*v.* figs. 132–137) I am inclined to interpret it as an element, *i. e.*, a fin support, transposed from a hinder position,* a view which is the less difficult to accept when one considers the metamorphosis to which the head roof has been subjected by the precocious growth of the eyes.



Figs. 110 and 111.—Skull and branchial arches of Shark and Chimæroid compared.

B^1–B^5, Branchial arches; *BH*, basihyal; *btr*, basis trabecularum (Kitchen Parker); *C*, copula; *CB*, ceratobranchial; *EB*, Epibranchial; *HB*, hypobranchial; *l'*, "anteriormost lip cartilage" (Kitchen Parker); *M*, mandible; *PB*, pharyngobranchial.

The history of the fins and their supports, finally, gives additional evidence as to the modified nature of later Chimæroid development. We may comment, for example, upon the appearance of lobate dorsal fins, the anterior with its spine, at an early period, and the prominence of the paired fins, the pectoral, for example, having at one time a greater proportional size than in the adult. We observe also the precocious appearance of the mixipterygia and the antero-pelvic appendages (note especially plate IX, fig. 50^f; also fig. 90, and Schauinsland's Taf. XVI, figs. 120 and 125), a well-marked character which in such early embryos can hardly be regarded as primitive. Nor is the plan of development of the paired fins to be looked upon as yielding any evidence in favor of Gegenbaur's archipterygium theory. Thus, the pectoral, for example, appears not as a lobate organ, contracted, shortly to bud out radial structures, but as a lappet of a lateral fold which shows in the early stages distinct metameral elements (*cf.* especially plate VIII, fig. 49, and Schauinsland's Taf. XXIV, fig. 174).* The paired fins, in short, develop like those of

*This translocation of anterior fin-rays is by no means uncommon, associated, too, with change of function, *e. g.*, Lophius, Antennarius, etc. Even the sucking disc of Remora might here be cited.

young sharks, save that, as in the case of many other chimæroid structures, the rate of growth is accelerated; the lateral-fold beginnings extend over fewer body segments and are higher (proximo-distally), leading us to conclude that in this mode of early fin growth the Chimæroid exhibits the same relation to the shark that the teleost bears to the ganoid. Especially convincing evidence as to the modified nature of the chimæroid fin is produced by the development of the ventral "claspers"; for these, the antero-ventral hooks and the mixipterygia, are to be regarded as highly modified radials. The antero-ventral clasper, it is clear, has not yet been evolved in the sharks, unless the greatly enlarged anterior lappet of the ventral fin be regarded as its equivalent; but there is good foundation for the belief that in Chimæroids between the antero-ventral organ and the compressed lappet of the

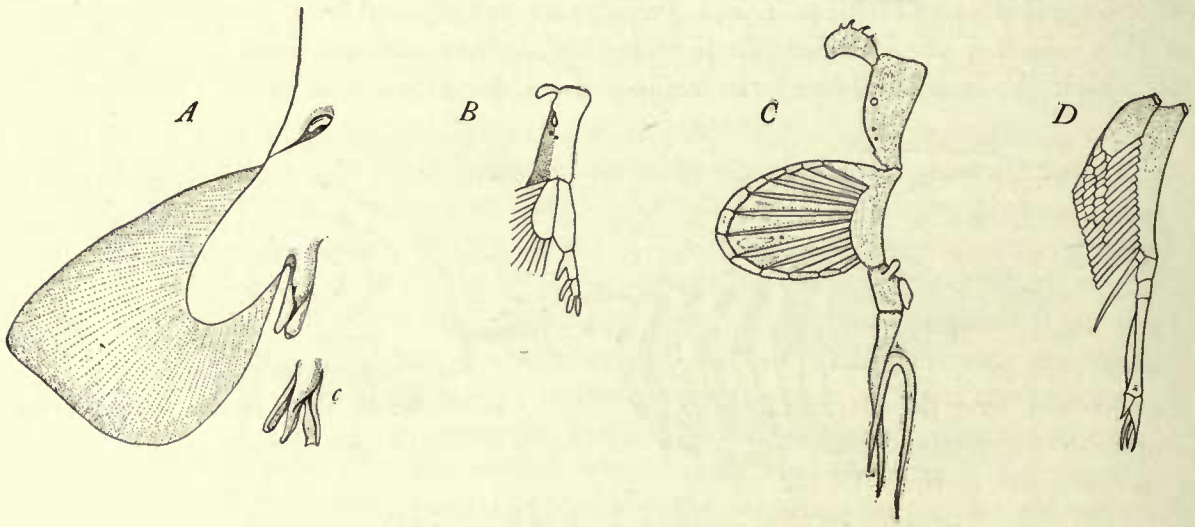


Fig. 112.—Ventral fin and appendages in Chimæra colliei.

A, Fin of young specimen (31 cm. in length); ventral aspect showing mixipterygia and antero-ventral clasper, the latter still connected by dermal crease with the anterior rim of fin; c, mixipterygium with lips unfolded; B, skeleton of foregoing fin, showing the arrangement of the supports (radials) of the branches of the mixipterygium; C, skeleton of fin, adult; D, skeleton of ventral fin of Cestracion (Heterodontus japonicus), adult, for comparison with foregoing.

pelvic fin there formerly existed a number of radialia; witness, for example, the rudiments of the segmentation of the basal plate from which the antero-ventral organ arises (fig. 112, nerve and vessel openings in B and C),† or better still, the radials which persist in the anterior reach of the fin of the Jurassic Chimæroid, Squaloraja (fig. 138, *ar*). The mixipterygium also bears testimony to having been closely connected with the radials of the base of the fin; thus in one stage in development, *cf.* fig. 112 B, the base of the mixipterygium bears rudiments of radialia, and the trifid tip is in itself a relic of a clustering of distal radials. These observations are clearly in line with Jungersen's, who, while admitting that the "appendix-skeleton of the Holocephales is of less compound construction than that of Plagiostomes," calls attention to the "wide separation of the whole organ (*i. e.*,)

*In the adult Chimæroid the basal articular element of the pectoral fin is usually termed (as in Cestracion) mesopterygium, and it is regarded (Gegenbaur, 1901) as including also the propterygium; Schauinsland, however, has shown (*op. cit.*, Taf. XXIV, fig. 174) that the bibasal character of the fin is due to the obsolescence of the metapterygium. The articular basal is, therefore, the propterygium. With this result the present writer is in accord.

†This conclusion was originally suggested by Gegenbaur (1901) on the evidence of adult anatomy.

the mixipterygium) from the fin proper; the highly specialized form of the primary skeletal parts—against the simpler form in the Plagiostomes (as the simple rod-like shape of the terminal joint * * *),'' the presence of ''particular copulatory organs,'' and infers finally that ''the Holocephales by no means occupy a primitive position among the Selachians.'' (Danish Ingolf Exped., II, pp. 20–21).

VISCERA.

In the development of its viscera, also, Chimæra indicates a high degree of specialization. This, for example, may be noted in the following structures:

Mesenteries.—No continuous mesentery is observed even in later embryonic stages of development. Thus, in the embryo shown in plate VII, fig. 45, the mesentery is clearly reduced to the string-like supports for vessels and ducts which characterize the adult. In the same stage only a rudiment of a ventral mesentery is present.

Gut.—In no stage is the gut of the same proportional length as in the shark. In the latter (Pristiurus) the length of the digestive tract (measured from mouth to anus) decreases in length between stages K to O from 55 per cent to about 50 per cent of the total length of the embryo; in Chimæra in similar stages from less than 30 to about 15 per cent. In other words, the gut of Chimæra develops in a much more restricted body region; and from early stages it appears as a short tube of wide caliber. The stomach dilatation, we may thus conclude, fails to become expressed, and the intestinal valve, instead of undergoing the further spiral development of sharks, makes but a few turns (about four) and then increases rapidly in the width of the infolded band.

Gills.—The gills exhibit greater changes in their ''metameral'' series than sharks. Thus the hyobranchial cleft, even in as early a stage as K, is notably the largest and by stage O the opercular fold has attained almost its adult proportion. On the other hand, the fifth gill-furrow, although clearly indicated, *e. g.*, stages K, L, M, fails to become a functional gill-slit. And the spiracle, even in a favorable stage, is little more than a tubular rudiment; it never develops respiratory filaments and is lost by stage N. Another evidence of precocious development is shown in the mode of growth of the external gills. These filaments are from the beginning (about stage K) of large caliber (*cf.* Schauinsland's Taf. XIV, fig. 110), *i. e.*, they at once assume nearly their functional size. Accordingly they do not arise in a uniformly developed vertical series, but on account of their extraordinary diameter bud out one after another as the gill-bar increases in size. Their later specialization in developing blood-producing dilatations has already been noted (pp. 60, 106).

Kidney.—The restricted length of the visceral cavity is accompanied by modifications of the excretory system. Of the pronephros I am unable at present to give a detailed account, and will note only that it is smaller and more difficult to trace than in the shark. The mesonephric tubules, on the other hand, are long and coiled irregularly; they appear early and are clustered in a deep stroma along the dorsal wall of the body cavity. Their early condition, therefore, does not,

embryologically at least, indicate a primitive segmented condition (Redecke), and I am led to suggest that the "segmentation" of the kidney of the adult arose secondarily. The absence of the Geschlechtsniere in Chimæroids, moreover, I also interpret as a secondary reduction, an accompaniment of the enormous development of kidney in a short body cavity, a process which caused an enlargement of functional nephric tubules, an obliteration of rudimentary ones, and more direct and special means of carrying out gonadial products. In favor of the last interpretation are the great size and elaborate regional differentiation of Wolffian and Müllerian ducts.

NERVOUS SYSTEM.

The following features in the development of the system may be mentioned as indicating that the Chimæroids have been subject to wider changes than kindred sharks.

Reduction of Cord.—The cord in the region of tail and hinder trunk, representing about 60 per cent of its entire length, is greatly modified. Contrast in this region the diameter of the cord, its histological differentiation, the size, number, and character of the roots of the spinal nerves. The flattening of the cord in the hinder trunk and tail region is, therefore, hardly to be compared to the condition in Cyclostomes.

Flexure of Brain.—In Callorhynchus (*cf.* Schauinsland's Taf. XXII) the brain shows extraordinary flexures; in the region of the midbrain its axis changes direction by almost 180°.

Size of Infundibulum.—In early stages the infundibulum attains great size; and concomitantly the dorsal wall of the diencephalon is compressed between the forebrain and the optic lobes.

Separation of Hemispheres.—In this regard the early condition is more marked than in any other fish-like vertebrate. Observe also the separation of the entire forebrain from the midbrain. This in Chimæra begins in early stages and in the adult attains remarkable proportions.

III. FOSSIL CHIMÆROIDS:

THEIR SIGNIFICANCE IN THE STUDY OF RECENT FORMS.

The evidence of paleontology in the problem of Chimæroid descent is important, although one must frankly admit that it is still lacking in essential details, for not only are fossil Chimæroids rare, but they occur with but few exceptions in fragmentary form.

An outline of the distribution in time of the genera of Chimæroids is shown at the bottom of page 134. In this has been omitted reference to the supposed Silurian Chimæroid *Dictyorhabdus priscus* Walcott, for reasons which are stated below. Among the genera given, it will be seen that three, doubtfully Chimæroid, are Devonian, representing together about 16 species; one, probably a Chimæroid, is Permian, and four are exclusively Jurassic. From this time onward the greatest number of genera flourished in the Cretaceous, representing at least 50 species, and one of these genera, Ischyodus, extends from the Jurassic into the early Miocene. Another, a Cretaceous genus, Callorhynchus, is, as we have seen, represented by half a dozen species at the present time.

With this plan of distribution in mind, we may summarize our knowledge of fossil Chimæroids with reference especially to their advancing characters.

THE QUESTION OF A SILURIAN CHIMÆROID.

Palæozoic Chimæroids claim evidently our closest attention, and we should consider first of all the question of the "fossil Chimæroids" described by Walcott in 1885. At Cañon City, Colorado, in the Ordovician (Upper Silurian), the United States Geological Survey obtained a number of narrow, ribbon-shaped fossils which were described by Walcott as *Dictyorhabdus priscus*, and were regarded provisionally, on account of their general shape and transverse striation, as vertebral columns of a chimæroid fish.* In spite of the relative abundance of these fossils, however, no Chimæra-like dental plates, spines, or kindred structures were found, a condition the more remarkable since in the matrix there occur innumerable fragmentary "fish" remains. It is therefore doubtful whether so delicate a structure as the vertebral column of a Chimæroid would be preserved if no traces were present of associated spines, heavier cartilages, and dental plates. The chimæroid nature of the fossils, moreover, becomes more doubtful still if they are closely scrutinized.

*Walcott, it should be stated, refers doubtfully to their chimæroid nature. The "correlation is based entirely upon the resemblance between the fossil form and the calcified sheath of *Chimæra monstrosa*. This resemblance is too striking to be passed over, although there are certain differences that render it of less value in classification than at first."

In the type specimens (*e. g.*, one shown in fig. 113) we note that the calcified "rings," which were compared to the "centra" of Chimæra, are not rings at all, in the sense that they occur in, for example, Squaloraja, but suggest rather a series of more or less irregular lines of growth. These, indeed, are not transverse to the long axis of the fossil, but at one side pass obliquely into root-like processes, compared by Walcott to "lateral rib-sockets or supports," structures which, it must be admitted, are altogether unknown in chimæroid anatomy. The foregoing evidence, accordingly, seemed inadequate for associating this fossil with Holocephali, and an examination of the types in Washington did not yield me any more convincing basis of comparison. Nevertheless the very suspicion of a Silurian Chimæroid was of sufficient interest to warrant an attempt to secure more perfectly preserved material.

Accordingly, in 1896, I took the opportunity of visiting the type locality, and may now add the following details:

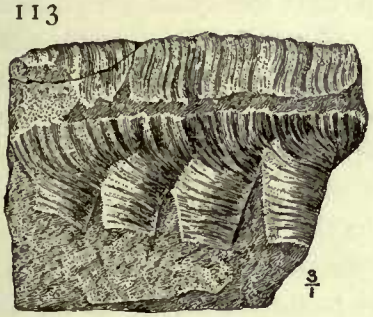
The horizon, the age of which is now generally admitted to be Ordovician, was readily located, and Dictyorhabdus was found to be fairly abundant. A day's collecting trip made in company with Mr. Burbadge of Cañon City, to whose kind guidance I am greatly indebted, resulted in obtaining about a dozen "columns" in lengths averaging between one and two inches, together with numerous fragments;

Distribution of Chimæroids in Time.

	No. of Species.	Devonian.	Carboniferous.	Permian.	Triassic.	Jurassic.	Cretaceous.	Eocene.	Miocene.	Pliocene.	Recent.
Ptyctodus	7	x									
Rhynchodus	6	x									
Palæomylus	3	x									
?Menaspis (=Chalcodus)	1			x							
Squaloraja	2					x					
Myriacanthus	2					x					
Chimæropsis	1					x					
Ganodus	1					x					
Brachymylus	2					x	x				
Ischyodus (=Aletodus)	25					x	x	x	x		
Pachymylus	1						x				
Edaphodon	27						x	x	?x		
Leptomylus	3						x				
Elasmodus	1						x	x			
Elasmodectes	1						x				
Mylognathus	1								x		
Callorhynchus	7						x				x
Harriotta	2										x
Rhinochimæra	1										x
Chimæra	8									x	x

and upon a closer examination of these remains, I was more than ever convinced that they could not be associated with a Chimæroid. In the first place, in well-preserved specimens the striæ are sometimes continued longitudinally above the "rib sockets," showing, in other words, that they were absolutely unlike vertebral centra. (*Cf.* fig. 114, *l.*) Furthermore, and this is, I believe, most convincing, several of the fossils showed a delicate flaring out at one end, like the mouth of a trumpet, which at once suggested the lip of a molluscan shell; a character in any event distinctly non-vertebrate, not to say un-Chimæroid. I am also permitted to state that it was the view of Professor Cope, to whom my specimens were shown, that the "columns" could have nothing to do with vertebrates. It is probable, on the other hand, that they represent fragments of the shells of mollusks, possibly Cephalopods.*

113



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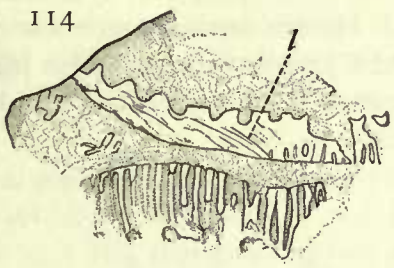


Figs. 113 and 114.—"Vertebral columns" of "Silurian Chimæroid," Dictyorhabdus priscus Walcott. The first figure after Walcott.
l, oblique laminæ in the structure of the fossil, suggesting lines of growth.

115

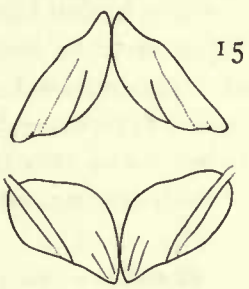


Fig. 115.—Dental plates of Menaspis armata = Chalcodus (permianus). Kupferschiefer. After specimen in Berlin Museum.

DEVONIAN CHIMÆROIDS.

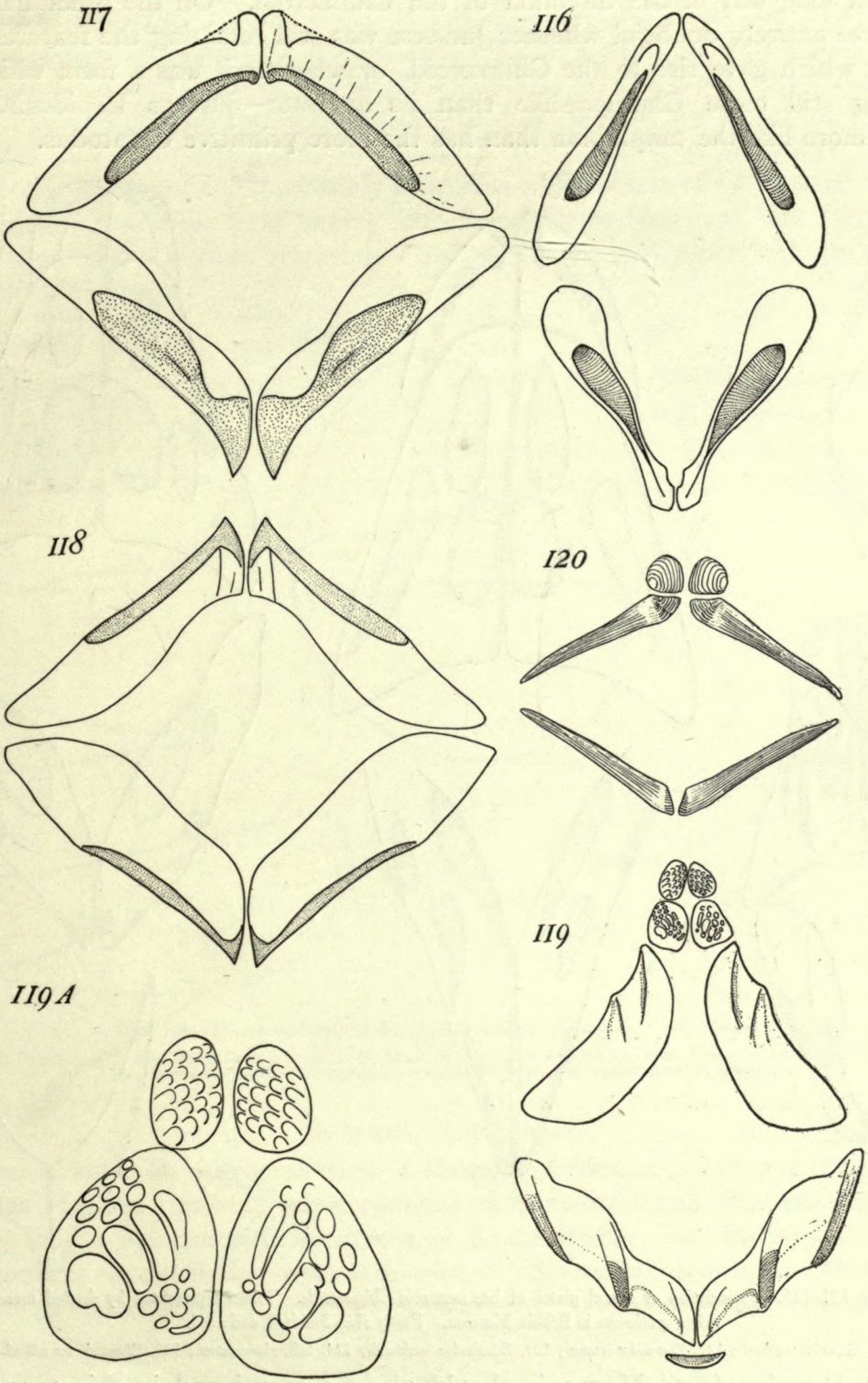
Chimæroid remains, or, more accurately, what are generally accepted as such, are widely distributed throughout the middle and especially the upper Devonian rocks of northern Europe and North America. These are referred to the family Ptyctodontidæ. Unfortunately for accurate diagnosis the fossils are fragmentary and the best results which can be obtained from them are briefly these: That in the three genera—all at present known—Ptyctodus, Rhynchodus, and Palæomylus, dental plates were present which resemble closely those of Chimæroids. On the other hand, these plates were only four in number and their tritoral characters are puzzling. Within the substance of the plate appear not a few tubercular tritors, but a general series of tritoral points, sometimes arranged in lamellæ, which in turn may form a series of flat or curving surfaces tritoral in function. The tritoral points are most conspicuous in Ptyctodus (fig. 116), where they form lamellæ. In Palæomylus (fig. 117) they spread out diffusely, and in Rhynchodus (fig. 118) are drawn together close to the rim of the plates, forming thus an extended sectorial

*The cephalopod nature of Dictyorhabdus was early commented upon by Hyatt, a reference which I had overlooked and for which I am recently indebted to my friend, Dr. C. R. Eastman.

margin. These conditions are shown in lateral (outer) aspect in figures 126–129. It may be added that there have been found (Eastman) a few detached plates of Ptyctodus (in the Hamilton limestone) resembling those of Myriacanthus as figured by Woodward (Cat. Foss. Fishes, vol. 2, pl. 2, fig. 2, *a*). Also that in Rhynchodus the shape of the meckelian cartilage is known (fig. 127). These characters, it will be seen, yield strong evidence in favor of their chimæroid nature. On the other hand, we must admit the possibility they may yet have belonged to some early specialized offshoot of a selachian stem which may not have given rise to true Chimæroids. Thus they may have greater affinity with the Sandalodonts, in which very similar tritoral points occur, or to Deltodonts or Cochliodonts, forms which on fairly strong evidence are regarded as selachian. As to Ptyctodontids it must frankly be admitted that there is nothing accurately known as to the form of body, character of fins, and the possession of spines. In the latter regard, however, it is fairly probable, as Eastman and others have shown, that the spine Phlyctænacanthus is to be regarded as belonging to Ptyctodus. And it is not impossible that Belemnacanthus and Heteracanthus were associated with members of this group. Harpacanthus and Cyrtacanthus may also have belonged to a Chimæroid. But spines of this character, we must admit, might be associated almost equally well with cestraciont sharks.

The main virtue in the study of Ptyctodontids is to the writer this—that they present some evidence (1) that Chimæroids are of Devonian stock; (2) that at this early period their dental plates were still but four in number, representing the dental structures of the jaw halves of sharks; and (3) that the tritors existed as small points forming together a texture in the dental plates which is well known among early sharks. The evidence, in short, leads us to conclude with fair probability that the vomerine plates of Chimæroids were a later acquisition.

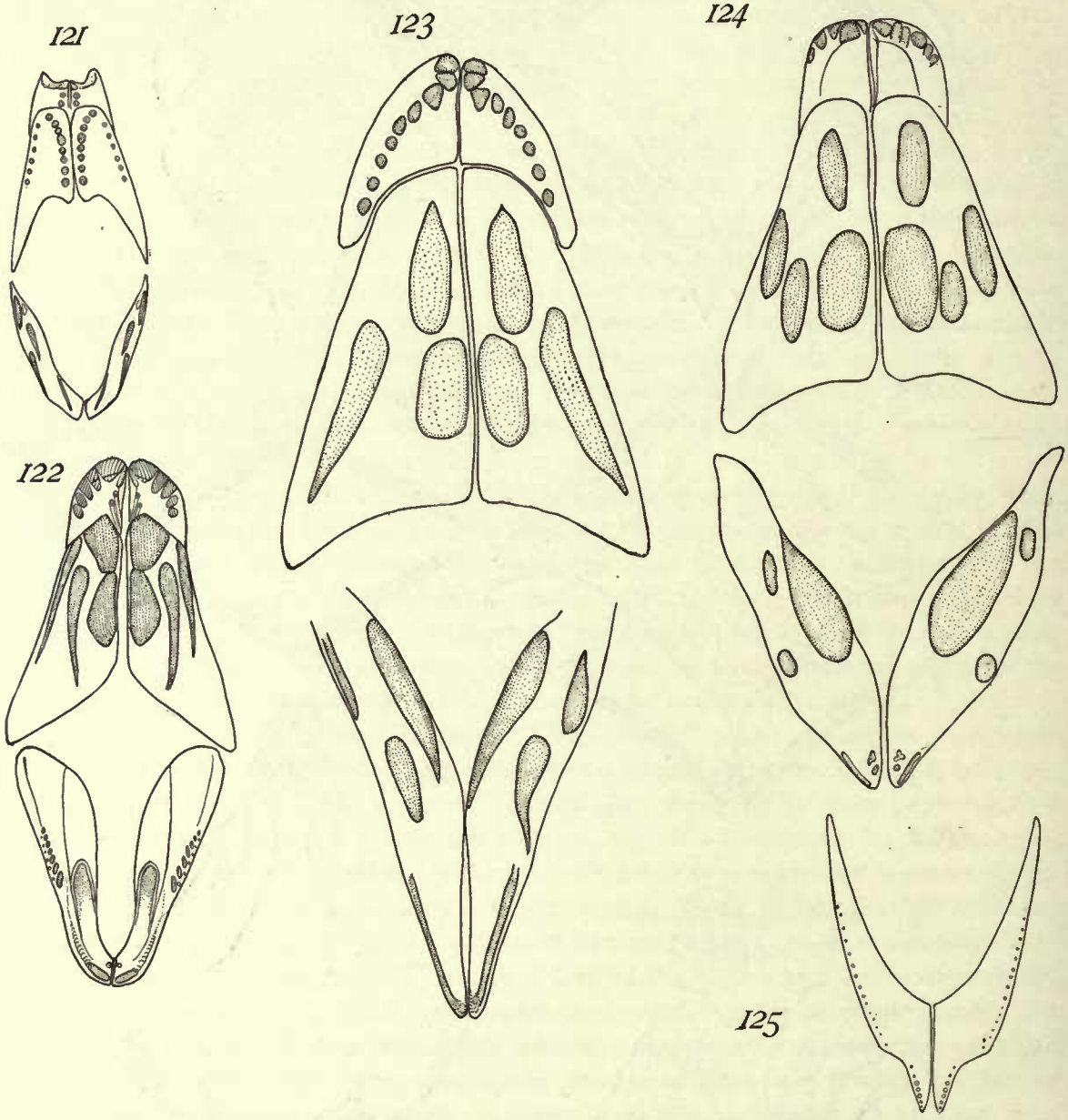
In connection with these earliest "Chimæroids" there should be mentioned the obscure group of Petalodontids, which occur abundantly throughout the Carbo-Permian and were in some regards Chimæra-like, though it is more probable that they represented forms of sharks which were not closely related to the ancestral Chimæroid, but were rather examples of parallelism. It is none the less noteworthy that in such a form as Janassa the dental arrangement, although still retaining discrete elements, suggests the formation of tritoral plates. Thus, we find that the dental elements are crowded into the axial line of the mouth and are here provided with interlocking ridges, which might well serve as the point of departure for the evolution of tritors. In this event, the tritoral points would represent not each one an individual tooth, but only a very small portion of a tooth. It may further be shown that Janassa was singularly chimæroid in the possession of a stout jaw, thick and solid at the symphysis, and of remarkably large labial elements. Finally, referring to Jaekel's reconstruction, it may be pointed out that Janassa possessed a distinct antero-ventral fin lappet which appears to the writer to correspond more accurately to the antero-ventral clasping organ of a Chimæroid than to an enlarged fin ray of Raja, with which Jaekel compares it. In short, there is at least the suggestion that in such a form as Janassa was represented a shark which had



Figs. 116–120.—Association of dental plates of early Chimæroids.

116, Ptyctodus, restored dentition, after specimens in Museum of Comparative Zoology, Cambridge, Mass.
117, Palæomylus, after specimens in Newberry collection, American Museum of Natural History.
118, Rhynchodus, after specimen in Newberry collection, American Museum of Natural History.
119, Myriacanthus, after specimens in the British Museum, and in the Jermyn Street collection; the tritoral areas of the two anterior pairs of plates in the upper jaw are shown in detail in fig. 119 A.
120, Squaloraja, after specimens in the British Museum, and in the Museum of Comparative Zoology, Cambridge, Mass.

evolved a long way in the direction of the Chimæroid. On the other hand, we must leave entirely doubtful whether Janassa was still retaining the features of an ancestor which gave rise to the Chimæroid, or whether it was a form which was becoming still more Chimæra-like than its ancestor—just as Lepidosiren has become more like the amphibian than has the more primitive Ceratodus.

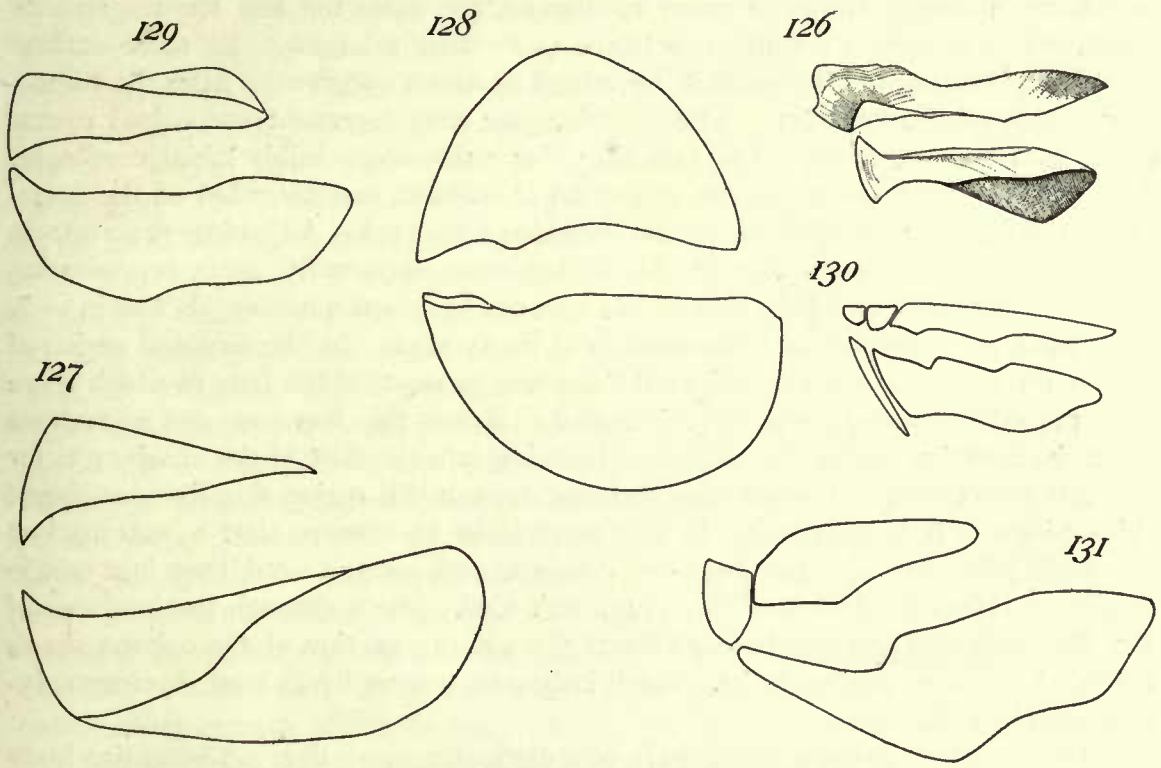


Figs. 121–125.—Association of dental plates of late mesozoic Chimæroids. Tritors represented by shaded areas. After specimens in British Museum. Partly after Smith Woodward.

121, Ganodus rugulosus; 122, Elasmodus hunteri; 123, Edaphodon bucklandi; 124, Ischyodus egertoni; 125, Elasmodectes willetti.

The Permian fossil Menaspis should also be mentioned in this connection. Whether, however, it can be regarded as Chimæroid has already been considered by the present writer in a recent number of the American Geologist (vol. xxxiv, pp. 49–53). It was there shown that the size of the dental plates of Menaspis (fig. 115) indicates that the entire region of the fossil inclosed with spines is to be

regarded as belonging to the head. It was noted, further, that the peculiar fibro-cartilage spines, characteristic of Menaspis, may be interpreted as homologous with the so-called lip cartilages of the later Squaloraja; on the other hand, the paired head spines of Menaspis correspond with those later seen in Myriacanthus, although, naturally, they were less highly specialized. If, accordingly, Menaspis proves to be a Permian Chimæroid, it certainly simplifies the problem of Chimæroid descent. It indicates a shark-like form having four dental plates (fig. 115), like Deltodus or Sandalodus, and a dermal armoring which advanced *pari passu* with the development of the dentition.



Figs. 126–131.—Associations of dental plates in fossil Chimæroids. Lateral aspect.

126, Ptyctodus; 127, Rhynchodus secans (attached to the mandibular dental plate is shown the outline of the entire meckelian cartilage); 128, Palæomylus greenei; 129, Palæomylus crassus; 130, Myriacanthus paradoxus; 131, Ischyodus.

JURASSIC CHIMÆROIDS.

Our definite knowledge of early Chimæroids does not, however, begin before the Lias (Lower Jurassic), when remains of Squaloraja and Myriacanthus occur, notably in the fine-grained limestones of Lyme Regis. In this favorable matrix Squaloraja is so perfectly preserved, even in its cartilaginous parts, that we are enabled to reconstruct its essential characters. As shown in fig. 138, it appears as a somewhat flattened form; its vertebral column is strengthened with fine, closely set, ring-shaped thickenings which resemble those of a typical recent Chimæroid; the cranium is autostylic (Traquair) and bears in the male the frontal clasping organ, which here is long and spine-shaped (figs. 137, 137 A, 138, and detail in fig. 139), situated immediately in front of the eyes and folding forward. The orbits are large, and between them the breadth of the cranium suggests that the

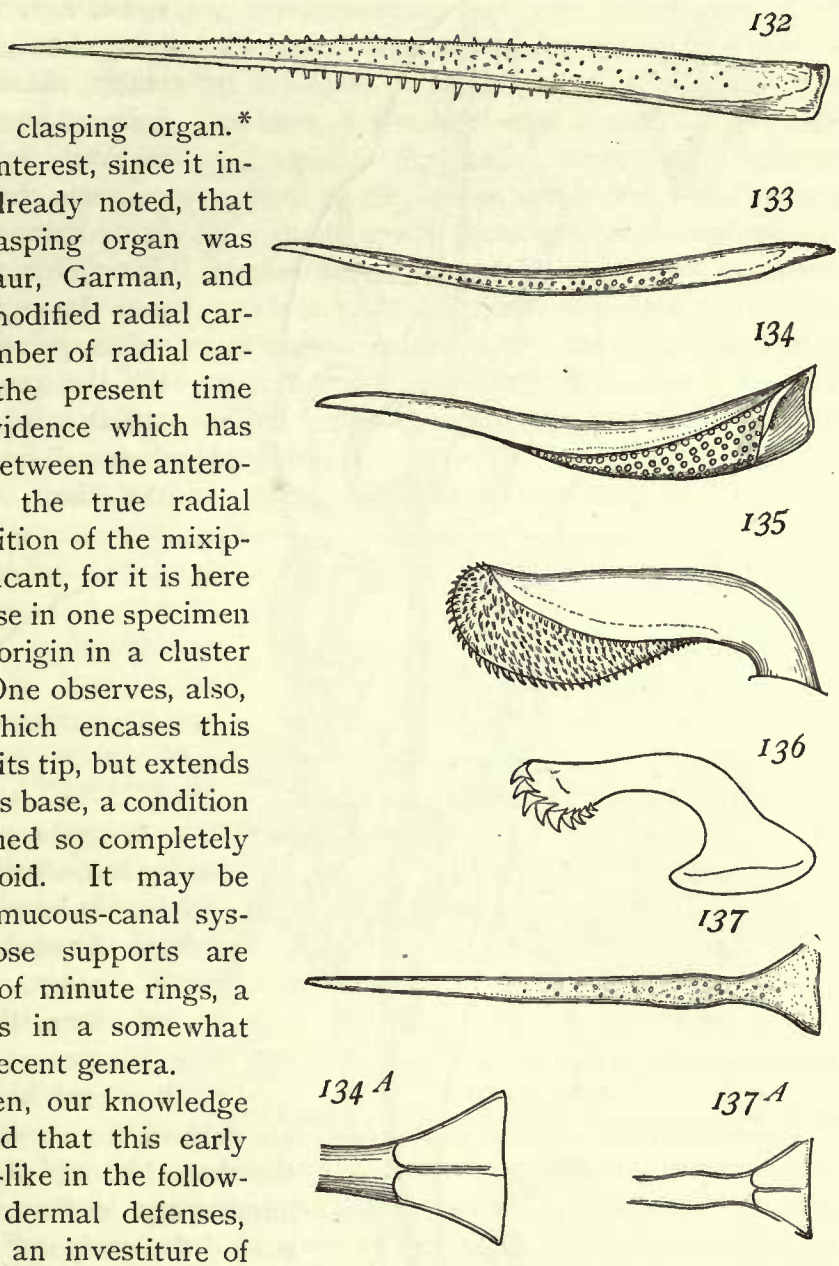
brain was shaped like that of a shark. Of dental plates (fig. 120) there are three pairs; the meckelian and palatines resemble one another closely, thus suggesting the doubtful Devonian forms. In front of the palatines now occur, for the first time among Chimæroids, a pair of "vomerine" plates, oblong and tumid. In these, as in the other dental plates, tritors occur, in the form of conspicuous lamellæ. The mouth was probably delicate and, judging from the position of the dental plates, it opened widely, far more shark-like than in any recent Chimæroid. At either side of the mouth region appear three conspicuous outgrowths, fibro-cartilaginous in structure, forming together the marginal framework of this region of the head. These structures, although shown in many specimens, are none the less too imperfectly preserved to warrant a definite conclusion as to their relations. By some authors they have been regarded as spines, by others as direct outgrowths from the trabecular region of the cranium. The anterior pair may represent the paired rostral cartilages of recent forms. The two posterior pairs are possibly labial cartilages. A conspicuous rostrum is present, unjointed at its base, and defended on the dorsal side by marginal rows of stout dermal denticles (fig. 139). Adjoining the rostrum the snout was narrowed, and in this region were apparently areas representing the pellucid spaces on either side of the rostrum in recent Chimæroids and in such selachians, for example, as Rhinobatus and many rays. In the occipital region of the cranium a large, median, elliptical fosse was present, at the base of which there were probably openings into the otic region. Below this fosse one can sometimes trace the anterior end of the column, advancing into the floor of the cranium as far forward as between the orbits, and showing even in this region ring-like peripheral thickenings. It is interesting in this connection to observe that a well-marked occipital joint was present between cranium and column, and that in a single specimen (Harvard Museum No. 1147, Pal. Coll., which through the kindness of Dr. Eastman was generously loaned me) the anterior portion of the column shows traces of a coarser segmentation, which indicates, outwardly at least, cyclospondylous vertebræ (fig. 138 A).

In dermal characters Squaloraja was distinctly shark-like. The entire body was covered more or less thickly with shagreen, and at certain points the denticles attained considerable size, *e. g.*, on the sides of the rostrum, near the base of the clasping spine (detail in fig. 139), along the sides of the tail, on the dorsal side, near the base of the paired fins, on the clasping organs, and almost as spines in the suborbital region. Here they form so firm a mass that the ring below the eye is preserved as a conspicuous character of the fossil.

Girdles and the cartilaginous supports of the paired fins are distinctly Chimæroid, *e. g.*, in location and proportions. The stoutly developed shoulder-girdle is similar in form to that of a recent genus; it is not known whether the bi-basal arrangement of the basalia occurs in the pectoral fin, but it is certain that the radial cartilages, about 30 in number, are arranged in a manner strikingly like those of Chimæra; their marginal extension was also modern in plan. In the ventral fins, on the other hand, more conservative conditions prevail, for the radial cartilages were probably 18 to 20 in number (about one-third more numerous than in recent forms),

and extended in their lines of attachment forward as far as the antero-lateral clasping organ.* This is of particular interest, since it indicates, as we have already noted, that the antero-lateral clasping organ was probably, as Gegenbaur, Garman, and Agassiz suggested, a modified radial cartilage (possibly a number of radial cartilages), but up to the present time there has been no evidence which has bridged the wide gap between the antero-ventral clasper and the true radial cartilages. The condition of the mixipterygium is also significant, for it is here short and wide, its base in one specimen suggesting clearly its origin in a cluster of radial cartilages. One observes, also, that the shagreen which encases this organ is not limited to its tip, but extends proximally almost to its base, a condition which has been retained so completely in no living Chimæroid. It may be noted, finally, that a mucous-canal system is present whose supports are arranged in rouleaux of minute rings, a condition which exists in a somewhat rudimentary form in recent genera.

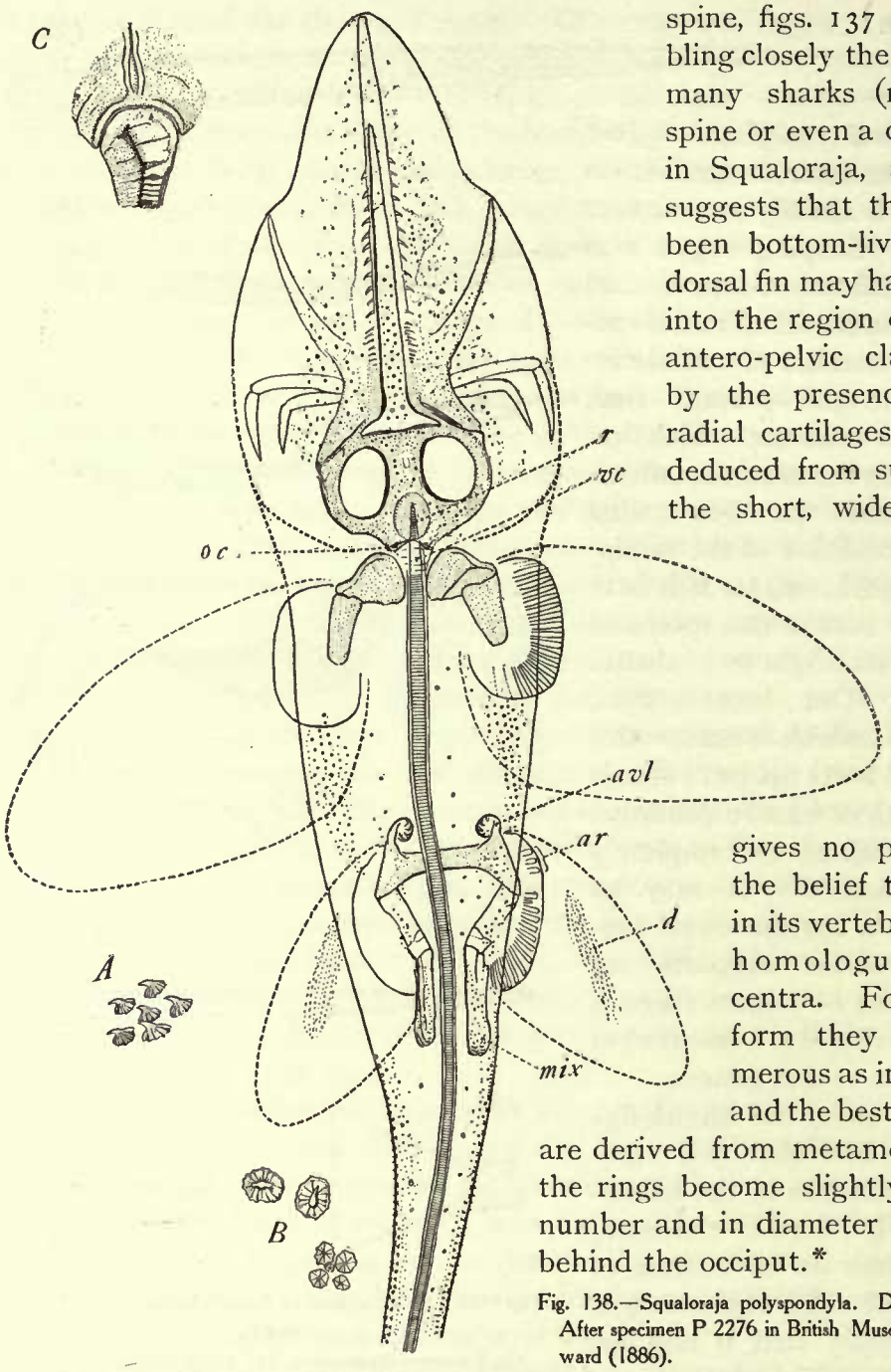
Summarizing, then, our knowledge of Squaloraja, we find that this early Chimæroid was shark-like in the following regards: (1) In dermal defenses, exhibiting as it does an investiture of shagreen. (2) In the width of the mouth, which shows definitely that it had not yet attained the beak-like character of the mouth of recent forms. (3) In the undifferentiated condition of the clasping organs. The frontal clasper is still a



Figs. 132–137.—Evolution of frontal clasping spine of Chimæroids.

132, Fin-spine of Myriacanthus. 133, Frontal clasping spine of Squaloraja. 134, Frontal clasping spine of Myriacanthus. 134 A, Base of clasping spine of Myriacanthus, ventral aspect, to show areas of attachment of muscles. 135, Frontal clasping spine of Ischyodus, after specimen in Munich Museum. 136, Frontal clasping spine of Chimæra, after section given by O. M. Reis. 137, Frontal clasping spine of Squaloraja, dorsal aspect. 137A, Ventral view of base, showing areas of attachment of muscles.

*This was observed by the writer in a specimen (P 2276) in the British Museum earlier described by Smith Woodward. Dr. Woodward did not, however, note that these clasping organs were present, although figuring them as "remarkably strong prepubic processes." Each clasper has appended denticles, of which as many as eleven were probably present. The same specimen has preserved in outline visceral structures, apparently testes and vasa deferentia.



spine, figs. 137 and 137 A, resembling closely the dorsal fin-spine of many sharks (no second dorsal spine or even a dorsal fin is known in Squaloraja, a condition which suggests that this form may have been bottom-living and that the dorsal fin may have become shifted into the region of the tail). The antero-pelvic claspers are shown by the presence of neighboring radial cartilages to be reasonably deduced from such elements, and the short, wide, shagreen-coated mixipterygia are also shark-like in pattern. Their derivation from radial cartilages is also indicated.

On the other hand, Squaloraja gives no positive ground for the belief that the fine rings in its vertebral column are the homologues of selachian centra. For in this Liassic form they are nearly as numerous as in the living genera, and the best evidence that they are derived from metameral centra is that the rings become slightly reduced both in number and in diameter in the region just behind the occiput.*

Fig. 138.—Squaloraja polyspondyla. Details and partial restoration. After specimen P 2276 in British Museum, figured by Smith Woodward (1886).

The narrowing of the snout is indicated in specimen No. 1147 io Harvard Museum and in an undescribed specimen in the Museum of Science and Arts, Edinburgh. Fin outlines hypothetical. Details of dermal tubercles are shown in *A* and *B*. In *C* the ventral occipital region is figured after the above-noted specimen of Harvard Museum. Here the condylar region is admirably preserved; behind it centra appear at the right, neural arches at the left. And "ring" vertebræ apparently grade into metameral centra. *ar*, anterior radials; *mix*, mixipterygium; *avl*, antero-ventral clasper; *oc*, occipital condyle; *r*, anterior "ring vertebræ"; *d*, tract of enlarged dermal denticles.

*Since the foregoing was written additional light has been thrown upon the question of metameral segmentation in the column of Squaloraja; in the Harvard specimen already referred to, a coarse segmentation, which suggests outwardly cyclospondylous vertebræ, is well shown in the postoccipital region, fig. 138 c. It is not certain, however, that these coarse segments are serially homologous with the fine rings in other parts of the column; it is possible, as embryology indicates, that they belong to the outer chordal sheath.

The second Jurassic Chimæroid, Myriacanthus, is known, unfortunately, in less detail. Nothing has been definitely ascertained regarding its general shape or the structures of its trunk. But what is known of its head region shows that it possessed extraordinary features. The form of the head was, in general, like that of Callorhynchus, terminating in a long snout. This had a somewhat foliaceous tip (fig. 140), as in the recent genus, but, on the other hand, was broader, less acutely pointed, and studded dorsally with shagreen denticles and dermal plates.

The best example of a snout of Myriacanthus belongs probably to a specimen in the Jermyn Street collection, of which a sketch is given in figure 141. The figure, which shows the snout in dorsal aspect, indicates also the spine-like nature of the frontal clasping organ. This organ is shown again, in lateral view in fig. 133. There can be little question that in this genus the shagreen-like defenses seen in the head of Squaloraja are replaced by a number of conspicuous pairs of dermal plates, some of which attain a large size and are furnished with spinous outgrowths. Thus, for example, on either side of the jaw (slightly schematized in fig. 142) there is a conspicuous "trachyacanthid" spine bearing a large serrate row of four or five subspines. These elements, it may be remarked, are well shown in a second specimen from Lyme Regis, in the Jermyn Street collection, and in Egerton's type specimen of *Prognathodus guentheri* (*Myriacanthus paradoxus*), now preserved in the British Museum, in which one of these spines is shown *in situ*, attached to the broad jaw. The arrangement of the dental plates of Myriacanthus is known with fair accuracy (fig. 119). The mandibular plates show foldings on the visceral face and in these folded areas appears the most conspicuous aggregation of tritoral points. A somewhat similar condition prevails in the palatines. In front of the palatines, as in Squaloraja, there occurs a pair of "vomerine" plates. These, however, instead of exhibiting a finely arranged series of tritoral points, present three rows of larger tritors, somewhat as indicated in the restoration (fig. 119 A). Furthermore, in front of the "vomerines" (and this condition is unique among all other Chimæroids, fossil or recent) there is a third and still smaller pair of plates, showing faintly a series of rows of tritors. Another puzzle in the dentition of Myriacanthus is seen in the region of the mandibular symphysis, for here occurs an azygous chisel-shaped tooth which is known only in this genus and in the kindred Chimæropsis (*cf.* also p. 145). The restoration in lateral view of these dental plates is shown in fig. 130. On the other hand, Myriacanthus, like recent Chimæroids, was autostylic, and it

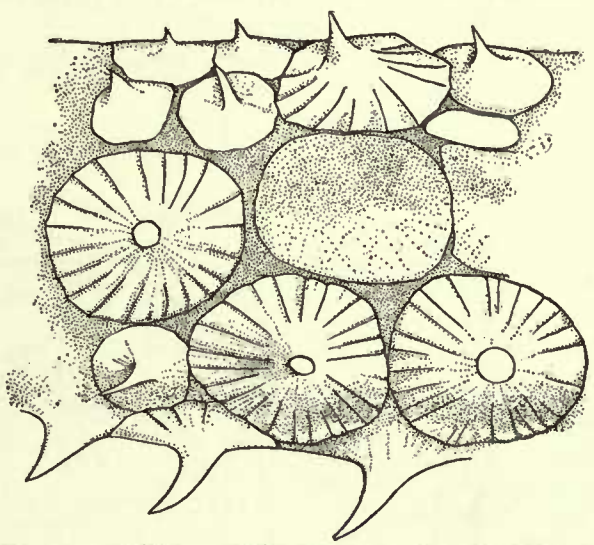


Fig. 139.—Squaloraja. Detail of rostral spine of specimen P 4323 in British Museum.

The dermal denticles are grouped closely together, their bases flat and greatly enlarged. They occasionally become detached, as the scars in the specimen indicate.

was provided with a well-marked dorsal fin which was supported anteriorly by a spine. This fin, it may be remarked, is the earliest dorsal known in Chimæroids, and its structure, therefore, deserves more than passing mention. Thus, as shown in fig. 140, and in the series of figures, figs. 143 A, B, C, D, its position is further hindward than in recent forms, in this regard suggesting interestingly the condition of shark. It is also noteworthy that the base of the myriacanthid spine is not articulated to the fused mass of anterior epichordalia, but is still connected with a hinder independent plate, *b*, which, we suggest, becomes in recent Chimæroids the articular process of the anterior cartilaginous plate. A further correspondence with a shark-like condition is noticed in the separation of the fin basis into proximal ("basal") and distal ("radial") moieties; in recent Chimæroids these are represented by but a single plate, *c*.

It should be finally observed that the vertebral column of Myriacanthus, fig. 143 B, shows anteriorly a segmentation which reasonably indicates the presence of centra.

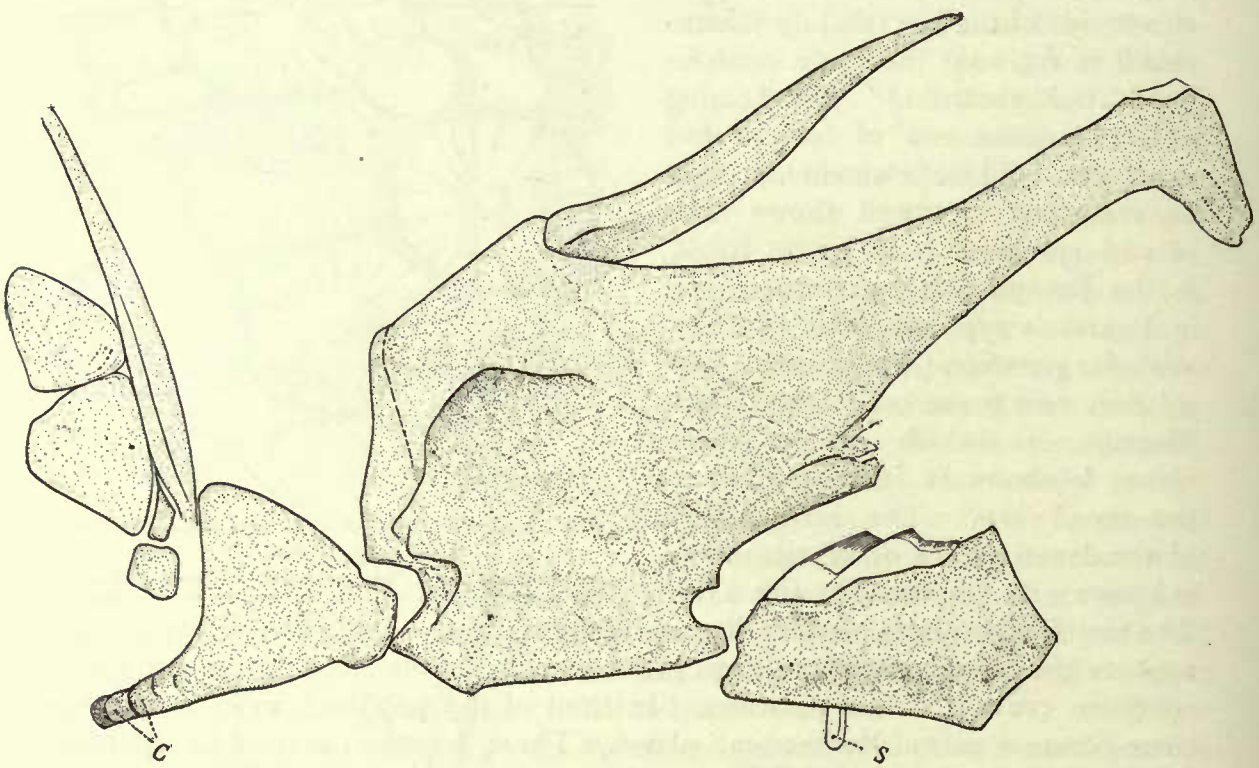


Fig. 140.—Head region of the Jurassic Chimæroid Myriacanthus. After Egerton's specimen, in British Museum.
C, Centra; *S*, Detached ventro-median chisel-shaped "tooth."

Summarizing our knowledge of Myriacanthus, we note that its dermal defenses are far more highly specialized than in Squaloraja, and that it has evolved an additional pair of tritoral plates in the upper jaw, as well as a ventro-median element in the mandible. Furthermore, that its frontal clasping organ, although still spine-shaped, is less like a spine than in Squaloraja (*cf.* figs. 131, 132, and 133). On the other hand, in its dorsal fin and in its fairly evident vertebræ it is more distinctly shark-like than any other Chimæroid.

Chimæropsis, a third Jurassic genus, is known only from the lithographic stone (Kimmeridgian = Upper Jurassic) of Bavaria. It resembles Myriacanthus—as far, at least, as one can judge from fragmentary remains. It certainly had similar mandibular plates and the presymphyseal chisel-shaped element. It was provided with a similar frontal clasping spine and an elongated snout. It had also a series of dermal plates, as in the former genus, and in addition its trunk was studded with small, conical, radially-grooved denticles.

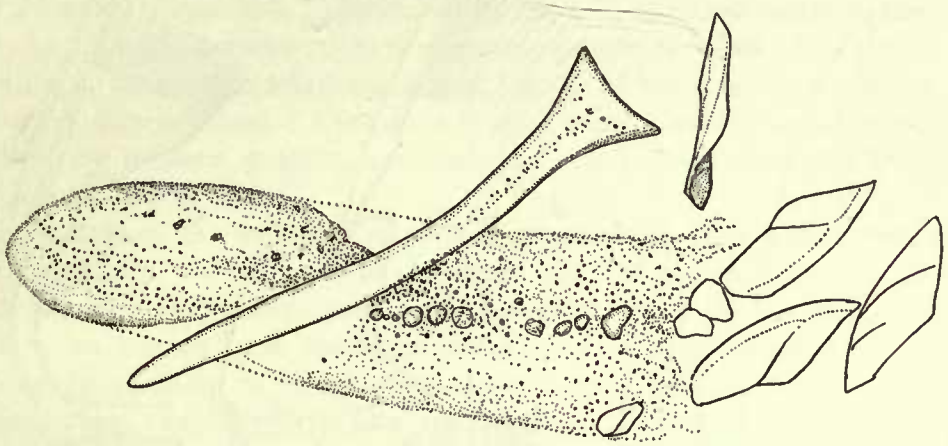


Fig. 141.—Myriacanthus granulatus. Detail of snout region.

After specimen presented to Jermyn Street Museum by Captain Ibbetson. As indicated in dorsal aspect, the snout is broad and thickly studded with dermal tubercles. The frontal clasping spine appears somewhat in its relative position. The dental plates are dissociated.

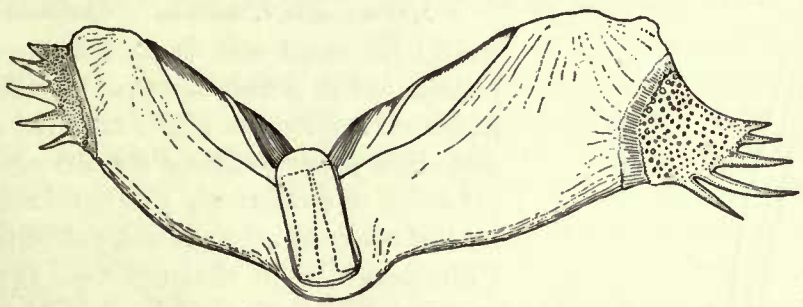


Fig. 142.—Mandible of Myriacanthus, viewed from in front.

Restoration after one of Egerton's specimens in the British Museum.

Brief mention need only be made of the Jurassic genera Ganodus (fig. 121) and Brachymylus, since these forms are known only by detached dental plates. It is possible, however, that a more or less complete skeleton of Ganodus* is preserved in the Museum at Northampton (Smith Woodward, 1892), and, in this event, its structures closely resemble Ischyodus.†

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*This specimen, a male, lacks the rostrum, but shows the frontal clasping organ ; of the latter the base is expanded transversely, and shows, as in Myriacanthus and Squaloraja (figs. 134A and 137A), a faint median crest on its attached face; its sides are laterally compressed. The column shows ring thickenings. Its dorsal spine is slender and arched (= Lepracanthus).

†Since the foregoing was written I have reexamined the specimen of "*Ganodus*" *avitus* in the Munich Museum, and am inclined to agree with its determination as Ischyodus by Reiss and Smith Woodward. It is quite possible, however, that this specimen will be shown to represent a new genus as soon as a more definite knowledge of Ischyodus is obtained. Thus the present specimen has small orbits, small snout, and large dermal denticles, the latter scattered widely, especially conspicuous in the region just anterior to the ventral fin. There is also ground for the belief that a pair of dermal plates were present on or near the posterior rim of the mandible.

Ischyodus, the final Jurassic Chimæroid, deserves more detailed examination, since its skeleton has been obtained in a condition of fair preservation in the Bavarian lithographic stone. From structural details, accordingly, this genus is known to be widely separated from Myriacanthus or Squaloraja; and on the other hand it resembled closely recent forms. It was thus similar in the shape of its head and

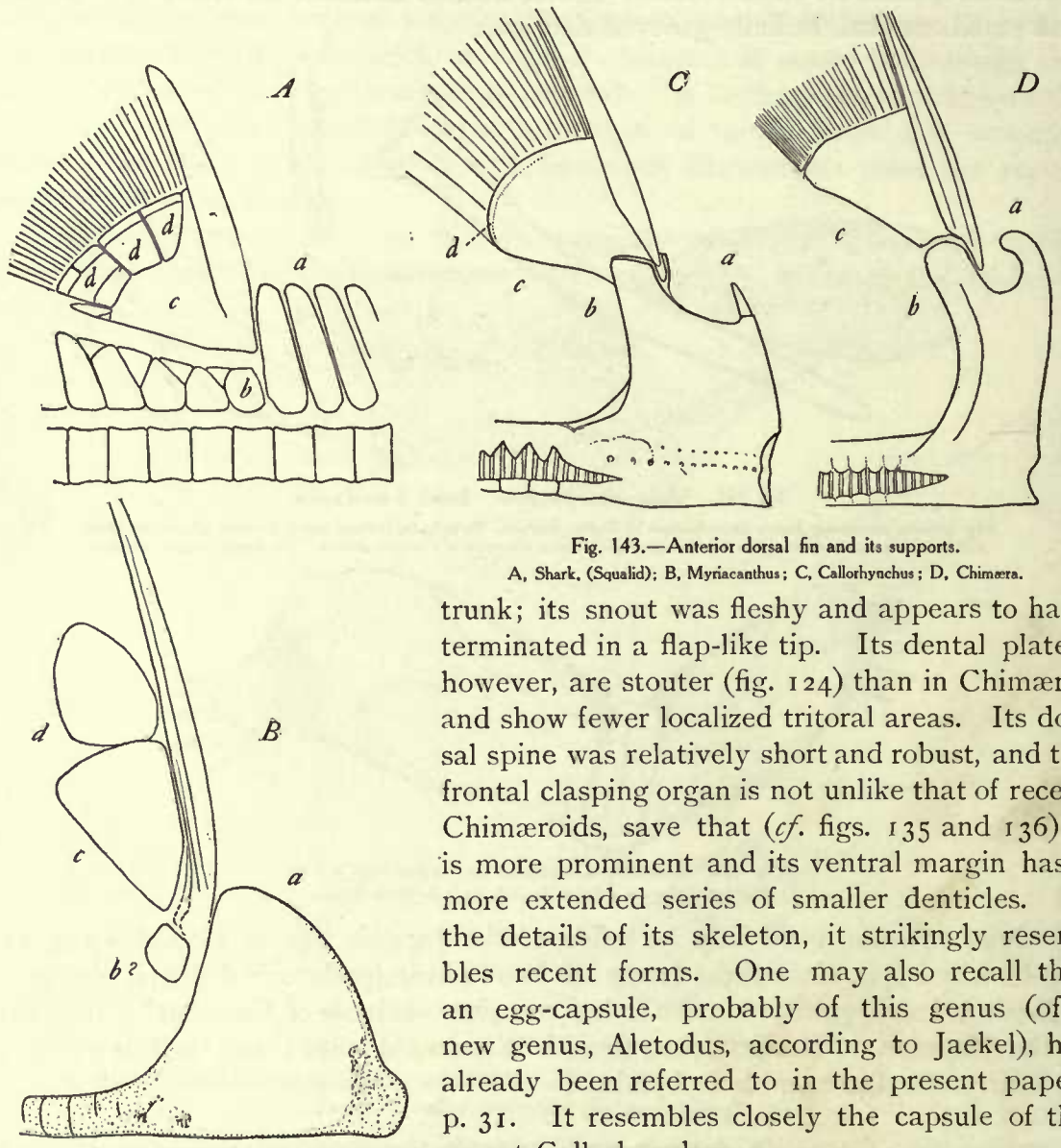

Fig. 143.—Anterior dorsal fin and its supports.
A, Shark, (Squalid); B, Myriacanthus; C, Callorhynchus; D, Chimæra.

trunk; its snout was fleshy and appears to have terminated in a flap-like tip. Its dental plates, however, are stouter (fig. 124) than in Chimæra, and show fewer localized tritoral areas. Its dorsal spine was relatively short and robust, and the frontal clasping organ is not unlike that of recent Chimæroids, save that (*cf.* figs. 135 and 136) it is more prominent and its ventral margin has a more extended series of smaller denticles. In the details of its skeleton, it strikingly resembles recent forms. One may also recall that an egg-capsule, probably of this genus (of a new genus, Aletodus, according to Jaekel), has already been referred to in the present paper, p. 31. It resembles closely the capsule of the recent Callorhynchus.

It is clear that in Ischyodus is represented the advancing line of Chimæroids, for it extends from the upper (probably, indeed, from the lower) Jurassic as far as the upper Chalk, even possibly into the Miocene (? *I. helvetica*), and is represented during this interval by many species of many sizes. Some were probably as small as the recent *Chimæra colliei*, others must have exceeded 3 meters in length.

CRETACEOUS CHIMÆROIDS.

Chimæroids, it may finally be remarked, were at their maximum evolutional development during the Cretaceous period; they were then represented by the greatest number of genera and of species (about 50 species), a result which may well have proceeded from the acquisition in their line of some new "expression points"; such, for example, may have been the apposition of meckelian and chisel-shaped subnasal "vomerine" plates, which must have added vastly to the effectiveness of this type of dentition; also the greater development of the clasping organs; also, perhaps, deep-water adaptations which enabled these forms to enter a new and rich field for development. Certain it is that these Cretaceous Chimæroids were of a distinctly modern pattern, and one of them is even assigned to the recent genus Callorhynchus.

The details of the evolution of recent genera from their Cretaceous ancestors are unfortunately meager. Dental plates and spines are practically the only evidence at hand for comparison. If, however, we limit our studies to dental characters, we can at least conclude that their evolution has been in the line of producing tritors either in marginal or in centralized arrangement. In Ischyodus, for example (fig. 124), it will be seen that some of the tritoral areas of the palatines and meckelian plates are becoming localized near the median line. In Edaphodon (fig. 123) the tritoral areas of even the vomerines are more nearly median; indeed the only conspicuous appearance of marginal tritors occurs at the tip of the meckelian plates. Elasmodus (fig. 122) indicates an interesting combination, since it has developed both the marginal and the median series of tritors. It has thus a dentition of a generalized character, and one is not surprised to find that it passes over from the Cretaceous into the Eocene. In fact, it differs little from the dentition of the recent Harriotta. On the other hand, Elasmodectes (judging from its meckelian plates, which alone are accurately known) represents a form which is specializing in the direction of marginal tritors; they are numerous, continuous in arrangement, and minute in size, and altogether the plates were probably beak-like in function. This type of dentition appears at first sight too specialized to have long survived. Nevertheless, granting a continued reduction of these minute marginal tritors, and more flattened and beak-like arrangement of the plates, a descendant of Elasmodectes might well be represented in the recent Rhinochimæra.

As far, therefore, as a study of the dental plates alone is concerned, one might conclude reasonably that the recent genera were descended from Mesozoic forms in somewhat the following way: Callorhynchus from an ancestor closely related to Edaphodon, Chimæra from Ischyodus, Harriotta from Elasmodus, and Rhinochimæra from Elasmodectes. Such genera, for example, as the Cretaceous Leptomylus and the Miocene Mylognathus are apparently already too specialized to have represented the ancestral condition of the living forms. There can be no question that, with the exception of the three genera first named, the Mesozoic, Tertiary and recent Chimæroids are a single and homogeneous stock. They have none of the

bizarre features of Myriacanthus, Chimæropsis, and Squaloraja; no highly specialized plates and spines in the head region, no spine-shaped frontal clasping organ, no presymphyseal element, and no second pair of "vomerine" plates. Among recent forms, Callorhynchus, a Cretaceous genus, has probably retained in most regards the striking characters of its Mesozoic kindred. And it is not to be wondered at, therefore, that its developmental features appear more conservative than in other genera. On one side of this early genus we may place Chimæra, which, as we have seen, is in many ways a highly modified form; and on the other side would be arranged Harriotta and Rhinochimæra, similar to one another outwardly, but (on the evidence of dental characters) long separated from a common ancestor.

It yet remains to consider the probable relationships of the earlier forms. It is clear, first of all, that in the Jurassic epoch there existed three distinct types of Chimæroids. One, as we have noted, is that of Ischyodus and its allies, from which unquestionably all recent Chimæroids are descended. The second, Squaloraja, represents an aberrant and terminal group; it is to its kindred as is Pristiophorus to sharks. On the other hand, one must admit that it shows certain characters* which ally it to the stock from which Ischyodus-like forms must have arisen. The third Jurassic type, represented by Myriacanthus and Chimæropsis, is the most difficult to interpret. From present data it can hardly have pictured the ancestral line of modern Chimæroids, for from what we already know of the elaborate dermal plates of the head and its "trachyacanthid" spines, we infer that it was already too highly specialized to have had the evolutional vigor to give rise to forms in which shagreen-like conditions again occur, for such a series would present an analogy not as close, *e. g.*, to the descending line of the sturgeons as to the line of the Cestracionts, in which the modern form is related only collaterally to the elaborately spined and heavily plated genera of the late Palæozoic. Especially puzzling are the dental characters of Myriacanthids; for how are to be interpreted the symphyseal chisel-shaped element and the anterior pair of subnasal plates? One might readily suggest that the former element was developed on the copula of the mandibular arch—a suggestion which bears with it a greater shade of probability when we consider the size and importance of the mandibular copula as recently described by both Schauinsland and the younger Fürbringer. And following a similar line of speculation we might maintain that the "vomerine" plates were developed on the pharyngobranchial element of the jaw arch, just as the palatine plates were developed on the next lower (epibranchial) element. In support of this hypothesis we may note that, as in Chimæra a pharyngobranchial element is present in the hyoid arch, a similar serial element appears also to have been present in the mandibular arch (*cf.* figs. 110 and 111). A second hypothesis—hypothesis may be a little too dignified a term—is that the "vomerine" and "prevomerine" plates of Myriacanthus represent the palatine plates of premandibular

*E. g., number and disposition of dental plates, clasping organs, integumental defenses.

gill-arches. This view, it will be seen, finds some support in the remarkable gill-arch-like character of the labial cartilages, and it becomes less fanciful when one considers how frequently the labial cartilages, especially in Chimæroids, have been homologized with premandibular arches. As far as Myriacanthus is concerned, such interpretations are clearly favored by our knowledge of its evident specialization in dermal defenses, for in such a light it would be not improbable that additional dermal elements would be evolved and impressed into the service of the mouth parts—*i. e.*, plates which may not have been present in the parent stock from which descended Myriacanthus, Squaloraja, and modern Chimæroids.

Moreover, it is worthy of mention that the forms which are commonly accepted as the earliest Chimæroids, the Ptyctodontids, have but two pairs of dental plates. For it might be plausibly suggested that these primitive forms had not reached the stage in evolution when the "vomerines" (*i. e.*, dermal elements) appeared as defenses for the anterior arch.

In accordance with the present considerations a scheme of the evolution of the genera of Chimæroids may be arranged somewhat as on page 150, fig. 144.

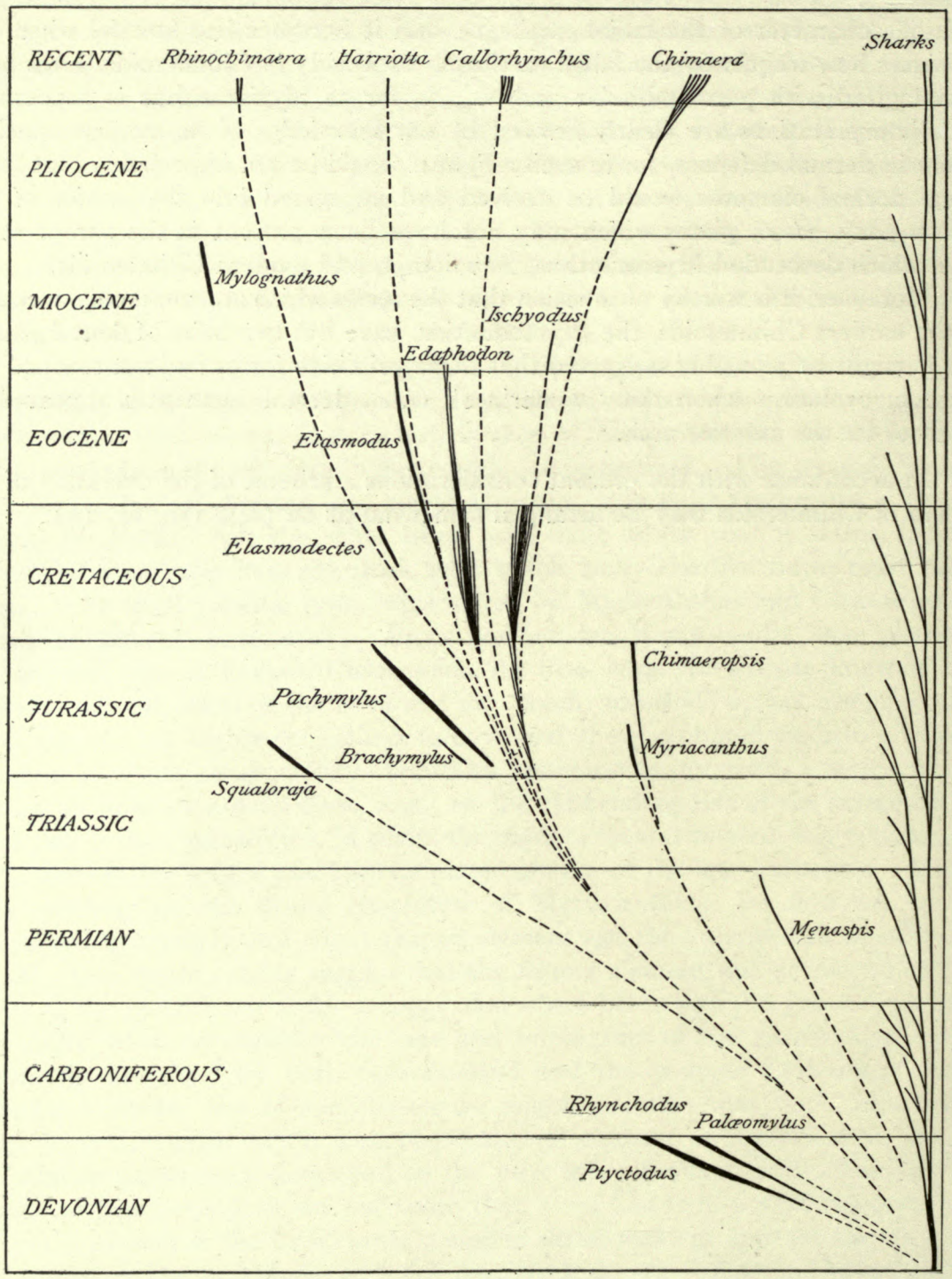

Fig. 144.—Phylogeny of the Chimæroids. Arrangement according to paleontological data.

IV. CHIMÆROIDS IN THE PROBLEM OF VERTEBRATE DESCENT.

On the basis of the foregoing discussion we may finally consider the critical question whether Chimæroids are to be regarded "as the most primitive vertebrates, or more precisely as the least modified descendants of the ancestral cranium- and jaw-bearing vertebrate?" Are they, in other words, to be looked upon as more primitive than sharks and as "representing a lower plane in piscine evolution"? These questions have been touched upon, more or less distinctly, throughout the present paper and the conclusion has been already indicated. And I think we may now state confidently that, from the evidence of embryology and paleontology, Chimæroids represent not the ancestral vertebrate, but rather a highly modified group descended from selachian ancestors. At the present time the evidence may be summarized upon which this induction is based.

PALEONTOLOGICAL EVIDENCE THAT CHIMÆROIDS ARE DERIVED FROM SELACHIAN ANCESTORS.

(*a*) *Their later origin:*

The earliest genera of whose Chimæroid nature there can be no doubt do not appear before the lower Jurassic, and from this horizon have been described but two genera. Sharks, on the other hand, appear in ages remotely earlier, and they are then represented by several orders, many genera, and very many species. Thus, in the Palæozoic alone, we may enumerate at least fifteen genera and forty species whose shark-like anatomical features are definitely known, and we may reject altogether the testimony of the numberless selachian "species" of spines and teeth. Into this limbo of indeterminata may provisionally be cast Ptyctodonts, together with Cochliodonts, Deltodonts, and similar forms. And we may in like manner regard the Permian Menaspis as doubtful. But even if we grant that all Ptyctodonts are Chimæroid, we have still the testimony that the sharks were in earlier periods overwhelmingly more numerous and more diversified. And we have equally to admit that, even at that early period, many sharks, from horizon to horizon, modify the character of their cuspid teeth in the direction of tritoral plates. In short, admitting the evidence of dentition, one may state conservatively, that even in their epoch Ptyctodontids stood to the sharks, both in number and in variety, only as one to one hundred. And from this testimony alone we can almost reject the thesis that Chimæroids were ancestral sharks. Unfavorable to the latter view, moreover, is the fact that the culmination of the Chimæroid line, *i. e.*, in genera and species, did not occur before the Cretaceous, while that of sharks antedated the Permian.

(*b*) *Shark-like morphological characters of early Chimæroids:*

The earliest definitely known Chimæroids were clearly shark-like. In this regard attention need only be called to the facts: (1) That they had shark-like dermal denticles scattered over the body; (2) a male clasping organ in the form of a selachian fin-spine; (3) rudiments of vertebral centra in the postoccipital region; and (4), in one form at least, tritors in the anterior dental plates which in arrangement resemble strikingly the teeth of a Cestraciont shark.

Furthermore, the earliest Chimæroids present no characters which can be fairly interpreted as more primitive than those of sharks. They were, on the contrary, more modified. Thus in their males they had already evolved the three sets of clasping organs.

EMBRYOLOGICAL EVIDENCE IN FAVOR OF THE VIEW THAT CHIMÆROIDS ARE DERIVED FROM SELACHIAN ANCESTORS.

The riddle of Chimæroid development can, I am convinced, be read in only one way; for the evidence yielded by the various phases of embryology points to the modified nature of Chimæroid descent: That is, if we grant the value of transitional stages in demonstrating the descent of the more complicated from the less complicated type, we may in the present case obtain a mass of evidence which must, it seems to me, be regarded as conclusive. The scope of this evidence is seen in the following summary:

I. Chimæroids are more complicated than sharks in sexual characters. Males differ from females to a greater degree in point of size and proportions, and in the development of clasping organs. Of the latter, sharks have only mixipterygia, while Chimæroids add to these the antero-ventral claspers (which are modified anterior radials of the ventral fin) and the frontal organ (which is interpreted as a transposed fin-spine).

II. The egg-capsule of the Chimæroid is the more complicated. It is larger in proportion to the size of the fish, and is adapted more especially to the needs of the young fish. In this regard we recall its remarkable regional differentiation (*i. e.*, for head, trunk, and tail of the young fish), breathing pores, opercular valve, and organ of attachment—characters more complicated than in the egg-capsules of sharks.

III. The early egg membranes are more complex than in sharks. Here we refer to the changes in the tunic and the behavior of its nuclei.

IV. The phenomena of fertilization. As one instance of complexity in Chimæra we recall that following polyspermy, the sperm merocytes divide at once amitotically; while in shark amitosis is attained only after a decadent series of mitotic divisions. Witness also, in the Chimæroid, the peculiar features of the sperm track and the character of the asters.

V. Early cleavage lines, as in the case of the (highly modified) rays, are suppressed, and the synchrony of segmentation is soon lost. Further complication in Chimæra appears in the germinal wall—in which are confused yolk-masses,

small blastomeres, merocytes and undivided yolk—and in the periphery of the blastoderm. We find further that amitosis occurs plentifully within the blastoderm.

VI. The fragmentation of the egg, which begins at gastrulation, doubtless arose as a primitive character, *i. e.*, holoblastism. Its function, however, in the modern Chimæroid has become a distinctly complicated one. By this process a large part of the yolk is diverted from its primitive use and is appropriated by the embryo secondarily, *via* gills and gut. The yolk-sac, accordingly, is reduced to miniature size.

VII. The embryo develops precociously. While still minute in size, *i. e.*, in terms of the blastoderm, it presents complicated structures; when 2.5 mm. in length it has already 25 somites, and suggests the adult. Compared to the young shark it is also more specialized in its relation to the germinal yolk and in the development of the vascular system. In this connection note also the differentiation of many types of merocytes, and the evidence that megaspheres are not primitive ova.

VIII. The head region of the embryo indicates precocious specialization. We thus note the early appearance and great size of the eyes, the appearance of the cephalic "hood," the greatly shifted position and the reduced size of the spiracle, the condition of the head mesoblast, the fewer and larger gill lamellæ, the moniliform character of the external gills, due to the presence of special blood-producing organs, the reduction of the fifth gill, and the early differentiation of the branchiostegal flap.

IX. The trunk region bears similar testimony in the matter of precocious specialization. We thus observe the early period at which the greatly elongated tail is produced, the anterior position of the anal region even in early embryos, the speedy obliteration of the lumen communicating between myo- and splanchnocœle, the early appearance of the dorsal fin-spine and of mixipterygia, the last a feature worthy of especial comment, since it indicates the appearance of secondary sexual characters in even small embryos. Also to be noted is the great size early assumed by the paired fins.

X. Larval characters are also developed prominently. To be mentioned in this regard are: Larval coloration; larval proportions of head, trunk, and fins; appearance of greatly enlarged dorsal scales; larval dentition, in which the outer rims of the dental plates become specially developed.

The foregoing are but the most conspicuous characters to be selected from the present embryological materials. Nevertheless there can be, I believe, no valid question as to their significance; for in no essential regard can they be interpreted as representing conditions so unmodified as to have given rise to the present conditions in the development of sharks.*

*One might, it is true, regard the modern sharks as arrested "larvæ" of Chimæroids, and thus maintain that shark embryos exhibit less complicated conditions than their ancestral forms. But if the diversity of specialized characters, as shown in the foregoing summary, is duly considered, this extreme view, it seems to me, can only fall of its own weight. For in view of the many lines of specialization of Chimæroids, it seems about as improbable that these forms could have represented the ancestral sharks as that a bird could have represented the ancestral reptile, or that a recent horse could have been the progenitor of Protohippus.

If this general position be granted, we have still to consider the question whether Chimæroids actually possess any primitive characters. Reviewing the materials at hand I think we may here refer to the following:

I. *Holoblastism.*—The egg cleaves totally. Of this there can be no doubt, although, as we have seen, this condition is complicated in many ways (pp. 58–63), and its retention is with strong probability due to the highly modified physiological needs which it now subserves. In other words, the holoblastism of Chimæra is less primitive than adaptive, and thus may not represent the ancestral condition in cleavage of such a form as the shark Cestracion (Heterodontus).

II. *Gastrulation.*—The appearance of the blastopore in front of rather than at the rim of the blastoderm is, I take it, of no little significance as a primitive character. Its retention is probably correlated with the survival of a holoblastic type of cleavage.

III. *Primitive conditions in the mouth region.*—No one, I assume, will deny that a pharyngobranchial element in the hyoid arch is a primitive feature. And of kindred significance are: The presence (1) of copular segments in the branchial arches, (2) of a mandibular copula, (3) of a pharyngobranchial process in the mouth arch, and (4) of more distinct "preoral arches" than in sharks. On the basis of these characters, then—and they are clearly of no little weight—may we conclude that Chimæra pictures more accurately than shark the ancestral gnathostome? To this conclusion there are clearly two lines of objections. First, that in many other features Chimæra is singularly modified, and, second, that the mouth region of Chimæroids is the less easily compared with that of recent sharks on account of the autostylism which has prevailed in the former groups since (at least) Jurassic times. In other words, in view of the first objection, it would be judicious, I conclude, to interpret the foregoing remarkable characters in the mouth parts of recent Chimæroids in the following way: That autostylism, although in itself a modified condition, tended less to alter the neighboring branchial structures than did the adaptation of a more flexible support for the jaw-hinge (*e. g.*, as in the modern sharks). And that thus, under the partially conservative influence of autostylism, Chimæroids, in spite of other structural modifications, have nevertheless retained a few of the characters of primitive sharks.

The foregoing conditions (I, II, and III) are, as far as I am aware, the most important findings of embryology as to the primitive position of Chimæroids. Less important in this question are the earlier data of morphology (*v.* pp. 4–5). Thus:

IV. *Absence of ribs.*—This character becomes of minor importance, in the light of developmental documents. The early shortening of the visceral cavity would obviously be unfavorable to the development of ribs, even if these elements had been present in the ancestral form. As to the latter condition, it may be mentioned that at the present time there is good reason for the belief that in the earliest sharks (Acanthodians and Cladoselachids) ribs were not present.

V. *Stomach, Kidney, Mazza's Glands.*—In these structures also the question of primitive conditions is by no means clear. For the early shortening of the visceral cavity may readily have been accompanied by secondary modifications in the viscera.

VI. *Musculature.*—The muscles of the branchial arches, like the arches themselves, retain primitive features; thus the adductor of the jaw retains its interbranchial character. On the other hand, there is no ground for the belief that the muscles of the shoulder girdle are unaltered; Gegenbaur (1901), for example, frankly admits that they are more modified than those of sharks, and he calls attention to the general blending of the segmental muscles of the trunk. There appear also in Chimæra special muscles developed in connection with the erectile spine and clasping organs which can best be interpreted as derived from the simpler elements in sharks.

VII. *Nervous System.*—In this connection it may be remarked that some of the primitive characters of Chimæra—open lateral line, separate nerve roots, simple auditory organ—are clearly paralleled in sharks, *e. g.*, Notidanids.

SUMMARY.

Chimæroids, accordingly, are widely modified rather than primitive forms. The evidence contributed by anatomy, embryology, and paleontology is unmistakably in favor of this interpretation. And there can be no doubt that the recent forms retain less perfectly the general characters of the ancestral gnathostome than do living sharks. On the other hand, it must be admitted that Chimæroids have retained several characters of their Palæozoic selachian ancestors which modern sharks have lost. According to many converging lines of evidence we may indeed go so far as to conclude that the ancestral Holocephali diverged from the selachian stem near or even within the group of the Palæozoic Cestracionts.* Indeed, the recent Chimæroids and Cestracionts retain many features of kinship. Among these need only be mentioned at the present time approximations in dentition, labial cartilages, articulation of mandibles, structures of fins, and urogenital system. Even the complicated egg-capsule of Chimæroids finds its nearest parallel in the recent Cestraciont, a comparison often lost sight of on account of the spiral arrangement of the lateral webs in the capsule of the latter form.

From the standpoint of taxonomy, on the other hand, it must be clearly recognized that the Chimæroids have been separate from the early sharks for so long a time and have acquired such different characters that they are to be given a high rank among the divisions of the subclass Elasmobranchii, the equivalent, let us say, of such groups as pleuracanths or pleuropterygians.†

*This conclusion recalls the remarks of W. K. Parker, in his paper on the skull of cyclostomes (Phil. Trans. 1883, p. 451): "Even the Chimæroids come so near the ordinary Elasmobranchs as to suggest that their embryology would not be so helpful (in the matter of the descent of the Cyclostomes) as one might imagine, especially if their solid upper face has been acquired as a secondary modification and not a *primary* condition, such as we see in the Tadpole, which is especially solid and largely continuous with the basis cranii, in the larval Aglossal types, Dactylethra and Pipa. (The interposition of those remarkable sharks, Cestracion and Notidanus, between the ordinary kinds and the Chimæroids, makes the likelihood of the solidity of the upper jaw being *primary* a very doubtful thing; I once thought otherwise, but found Mr. Balfour strongly set against me in this suggestion.)"

† One recalls at this point an early remark of Huxley: "For, considering, in addition to the cranial characters, the structure of the vertebral column, and of the branchiæ, the presence of an opercular covering to the gills, the peculiar dentition, the almost undeveloped gastric division of the alimentary canal, the opening of the rectum quite separately from and in front of the urogenital apertures, the relatively small and simple heart, the Chimæroids are far more definitely marked off from the Plagiostomes than the Teleostei are from the Ganoids."

Of the interrelationships of the various modern Chimæroids enough has been said in the foregoing pages; on many grounds it is evident that Callorhynchids have retained more nearly the characters of the ancestral Holocephali than have Chimærids.

If, finally, the data of Chimæroid development be carefully scrutinized, there will, I am sure, be found material for interesting reflection. For such a study brings with it considerations of greater significance than the pedigree of a group of little-studied vertebrates. It touches, first of all, the larger problem as to the degree to which embryology may be used in determining the kinship of animals. Moreover it furnishes somewhat definite illustrations of the processes—usually so obscure—of "shortening up" or "concentrating" developmental stages, and of embryonic "specializations." It also contributes, but in a minor degree, to the problem of germinal layers and, in even a more difficult field, to the interpretation of amitotic cell-division.

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LITERATURE LIST.

(*Omitting references to a number of text-books and early works.*)

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[In preparing the present summary the author acknowledges his indebtedness to Smith Woodward's Catalogue of Fossil Fishes in the British Museum, Vol. II.]

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EXPLANATION OF PLATES.

Plate I.

The Depositing of the Egg of Chimæra colliei.

(All figures about natural size.)

a. Anus.
c. Crease in tumid eminence in median ventral line, just posterior to opening of oviducts. Fig. 2.
c. Crease in oviduct in which marginal web of capsule was laid down. Fig. 4.
c. a. Tumid eminences formed by prolapsed ends of oviducts.
c. f. Capsular filament.
c. o. Capsular organ of attachment.
c. s. Cardinal sinus. (Margin of.)
f. Funnel of oviduct.
h. Heart.
l. Liver.
l. g. Lime gland.
m. Cord representing rudiment of dorsal mesentery, and containing the posterior mesenteric vessels.
o. Ovary.
op. Opening of oviducal sinus into cardinal sinus.
ovd. Oviduct.
ovd. a. Oviducal artery.
ovd. s. Oviducal sinus.
p. Urinary papilla.
r. Folds at lower end of rectum.
r. s. Receptaculum seminis.

Fig. 1.—Preparation of gravid female, showing eggs in oviduct. The egg-capsules are well formed, the egg-containing portion situated in the hinder portion of the oviduct. The external openings of the oviduct protrude from the body. The receptaculum seminis is shown at *r. s.* The oviducts extend far forward; their single opening appears at *f.*, immediately behind the position of the heart, *h.* The mesovarium is greatly restricted; it can, however, be distinguished on the left side of the figure where the capsular gland has been drawn out. The oviducal artery is extremely conspicuous at this stage.

Fig. 2.—Region of ventral fins of a specimen which has recently deposited eggs, showing the prolapsed ends of the oviducts.

Fig. 3.—Filamentous end of egg-capsule showing bulb-shaped organ of attachment. After sketch by Professor Wilbur.

Fig. 3 *a.*—Filamentous end of similar capsule.

Fig. 4.—Preparation showing oviducts of a specimen about to deposit egg-capsules. The oviducts, as shown in fig. 1, pass back on either side from the median funnel, *f.* The one at the right in the figure is shown lying in a capacious blood-filled sac of the peritoneum, *ovd. s.* This sinus is slung from the dorsal wall of the body cavity: its sides (right and left) draw closer together as they leave the oviduct and approach the (dorsal) wall of the body cavity. And here appears finally a series of openings, *op.*, through which blood of the oviducal sinus obtains free communication with the cardinal sinus, *c. s.* It is evident, of course, that the oviduct, *ovd.*, is bathed in the blood contained in the sinus; and that it can well be seen only where it lies against the wall of the sinus, the blood then forming the dark-red masses at either side of the oviduct. The preparation has been made so that the external opening of one oviduct is retained. From it one sees protruding the narrow end of the egg-capsule. The opposite oviduct is shown opened. The details of the lime gland appear at *l. g.* Immediately below it from a transverse fold in the oviduct arises the viscid secretion, *c. o.*, which draws together posteriorly and becomes the capsular filament, *c. f.* One observes many creases in the wall of the oviduct. In the deepest, *c.*, the lateral web of the egg-capsule is laid down. The creases are especially noteworthy near the hinder opening of the oviduct. Here its muscular walls serve to hold the capsule as it hangs in the water while the remainder of the capsular filament is being developed.

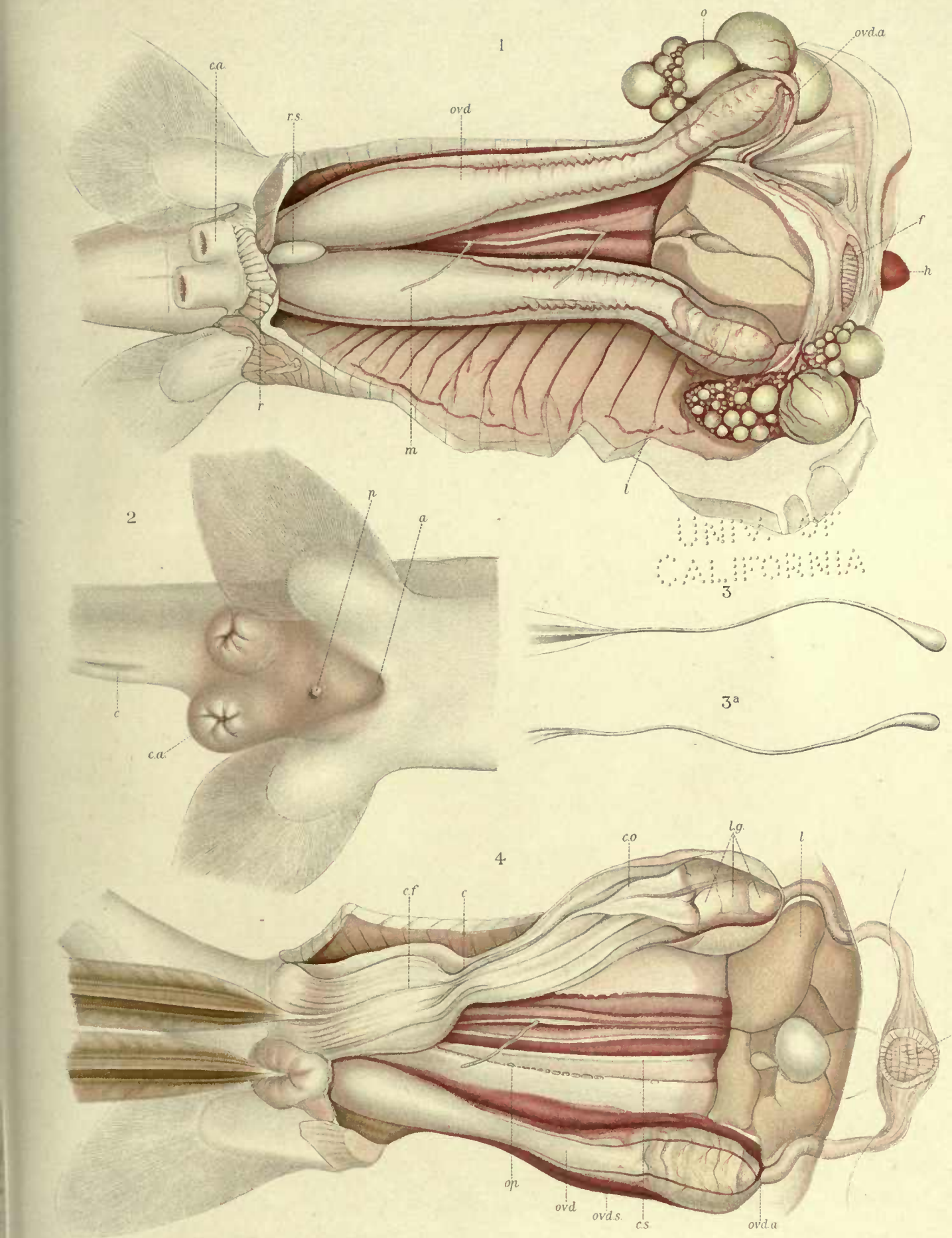

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Plate II.

Oviduct of Chimæra colliei and Mode of Formation of the Egg-Capsule.

(All figures natural size, excepting the last, fig. 11.)

a. l. Line in which the lip of the operculum separates from the side of the capsule.
b. Blastoderm.
c. Aperture (cervix) through which the anterior end of the capsule is beginning to protrude.
c. g. Capsular gland. In this region a series of transverse zones can be made out extending as far posteriorward as *t. o.*
c. p. Foldings in the margin of the capsule in which later appear the perforations in the caudal sheath.
d. k. Groove in which dorsal keel of egg-capsule is laid down. At either side of this are thickened areas which form the dorsal wall of capsule.
l. w. Folds in oviduct, in which the lateral web of the capsule is laid down.
m. Rudiment of mesentery of gut containing vessels. This lies behind oviduct (*cf.* plate 1, figs. 1 and 4).
m. o. Mesovarium.
o. Ovum about to break from the ovary.
ovd. Oviduct.
ovd. a. Oviducal artery.
ovd. s. Oviducal sinus.
r. Folds in groove of lateral web by which the rugæ of the capsule are established.
s. Stigma.
t. o. Folds under the edge of the lime gland in which the terminal organ of the filamentous capsule is laid down.
t. s. Thickened area in which is molded one side of the tail-sheath.

Fig. 5.—Ovary and oviduct of left side, showing egg about to be taken into the oviduct. The ovary is closely enveloped in the mesovarium, *m. o.*, the fold of which is continued back, encloses the oviduct and shows at *ovd. s.* the beginnings of the oviducal sinus. It will be observed that the egg, *o.*, about to escape from the ovary, is of great size. This is due to its fluid consistency at this stage, its contents having spread out when the preparation was made. A conspicuous stigma is present, to which nutrient blood-vessels converge. At this stage the oviduct is situated close to the dorsal wall of the cavity of abdomen. In later stages, during growth of the capsule, the oviduct hangs down freely into the abdomen and is bathed by the blood in the enlarged sinus, *ovd. s.*

Fig. 6.—Preparation of oviduct from which a developing capsule was removed, showing the foldings of the lining membrane which serve in modeling the capsule.

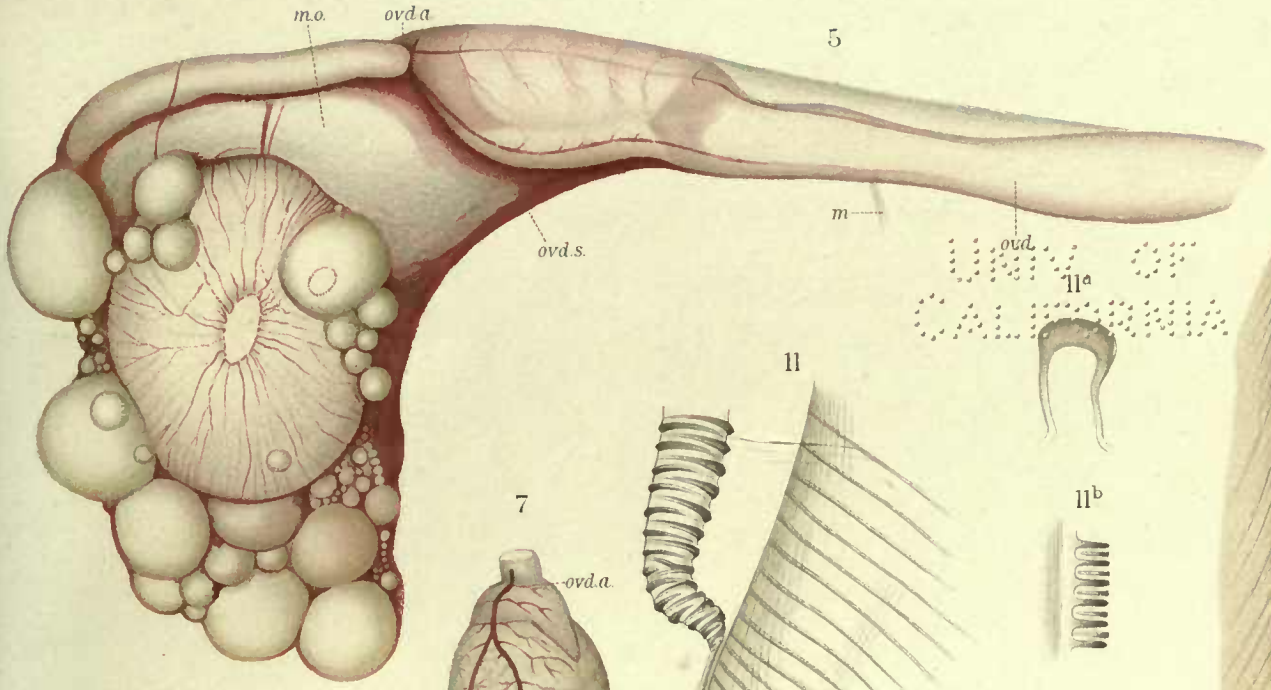
Fig. 7.—Preparation of anterior end of oviduct, showing a portion of the egg-capsule *in situ*. This figure illustrates the "segmental" character of the capsular gland, for each segment of which vessels are provided by the oviducal artery. The narrow end of the egg-capsule is shown within the oviduct; at *c. p.* foldings are shown in its marginal walls, which later produce the perforations of the caudal sheath. At either side of the deep groove, *d. k.*, in which the dorsal keel of the capsule is molded, appears a mass of glandular tissue. This is outrolled on either side into the marginal creases in which the lateral web of the capsule is being laid down.

Fig. 8.—Immature capsule containing egg. The tail end of this capsule was incomplete, but by means of a ligature it was so preserved that the egg was incubated. By the tension of the ligature, however, the shape of the capsule was somewhat altered and the egg became more spherical in form. The lateral web of this capsule is delicate and extremely wide.

Fig. 9.—Egg-capsule opened, showing shape into which the egg is elongated during incubation.

Fig. 10.—Egg-capsule at about the time of deposition, defective only in its terminal filament. This was, in fact, deposited while the fish was in captivity. From this figure one obtains an idea of the translucency of the freshly deposited capsule.

Fig. 11 and Fig. 11 *a-c.*—Details in structure of egg-capsule. Fig. 11 shows a detail in the structure of the opening valve. The fold in the wall near apex of capsule, *a. l.*, passes upward and inward into a ridge, the walls of which are folded into thickened and thinner areas alternately. At *a.* a transverse section shows height of this ridge. At *b.* appears a lateral view of the same ridge, indicating how it is made up of alternating elements. By a process of weathering in the thin intervening areas fenestræ are formed which insure respiration and which later, by a continued process of weathering, break open the valve of the capsule. In fig. 11 *c.* is shown the continuation of this folding process, occurring at sides of tail region of capsule. By the weathering of the thin spaces between the folds respiratory openings are gradually formed.



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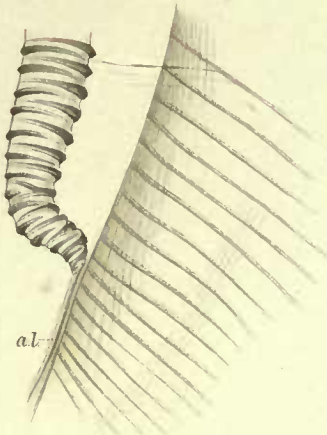

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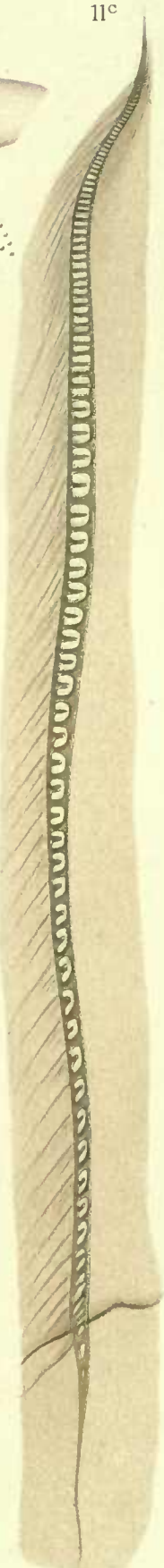

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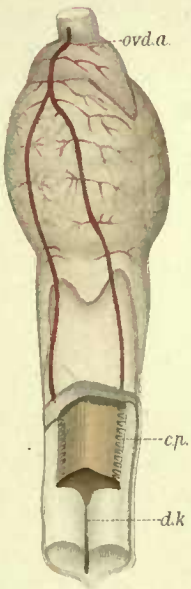

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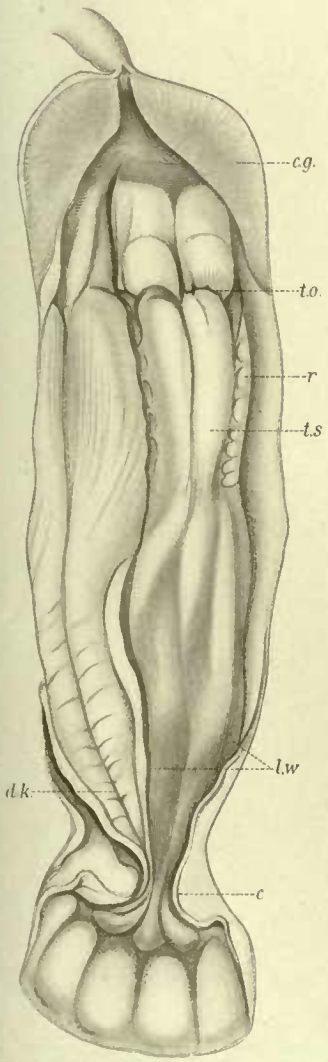

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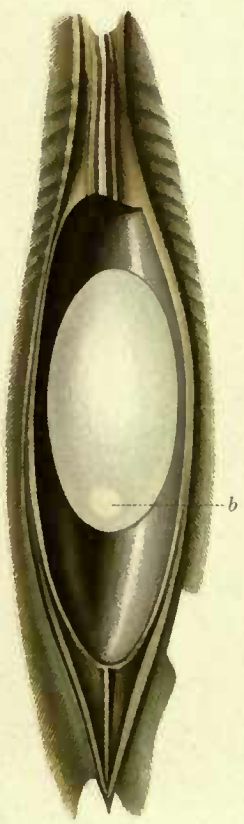

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Plate III.

The Egg-Capsule of Chimæra colliei Shown at Different Stages of Development.

(All figures about natural size.)

Fig. 12.—Capsule at the stage of the fertilization of the egg. The lowermost, *i. e.*, valve-bearing, end of the capsule is fairly complete, but its substance is delicate. The present capsule collapsed during the process of removing it from the oviduct; the egg it contained ruptured and flowed out through the unfinished end.

Fig. 13.—Capsule slightly older than the preceding. The opening end is of firmer consistency; the lateral web is well formed and somewhat pigmented.

Fig. 14.—Capsule slightly older than the preceding. The lateral dorsal webs are more perfectly formed.

Fig. 15.—Capsule in which the tail-sheath is beginning to be formed.

Fig. 16.—Egg-capsule in which the egg-inclosing portion is nearly completed. The tail-sheath is still a shapeless mass. The lateral webs are widest at this stage; they later become molded more closely and their delicate margins wear away soon after the egg is deposited. Rugæ are appearing near the posterior end of the capsule. An egg at this stage can be incubated if a ligature is placed near the base of the caudal sheath. (In figs. 12 to 16 capsules are shown in dorsal aspect.)

Fig. 17.—Egg-capsule from which embryo has been naturally hatched. This is the most perfect of the specimens which the writer dredged in Puget Sound. Its lateral webs are still largely uninjured, the filamentous tip alone being defective—lacking the bulbous organ of attachment. The ventral aspect is here shown, and we note at *d. h.* the enlargement of the wall of the capsule in which the mandibular region of the young fish comes to lie. The figure shows also the close laminæ in which the substance of the capsule is laid down.

Fig. 17 *a.*—Capsule of foregoing figure shown in lateral aspect. The valve of the capsule is represented as opened, a position assumed naturally only at the time of the escape of the young fish, the valve and its springy mechanism reminding one of the "mouth" of the corolla of a labiate plant. This figure shows the ridges, *r.* and *r'.*, which overlap (*r.* overlapping *r'.*) up to time the young fish escapes. It shows also how the neighboring tip of capsule weathers, leaving only three eminences protruding, of which the one belonging to the lid of the valve is the longest. The dorsal keel of the capsule is here well shown, *d. k.* It varies little in height and passes nearly the whole length of capsule.

Fig. 17 *b.*—Capsule of foregoing specimen shown in dorsal aspect. This specimen shows adequately the extent and character of the rugæ of the lateral web. At its anterior end, at *r.*, appears the rim of the valvular opening. In a capsule from which the fish has naturally escaped this ridge no longer returns to its former position under the ridge *r'*.

Fig. 17 *c.*—Capsule of foregoing specimen shown from in front. This figure was prepared to illustrate the character of the overfolded margins of opercular opening, and the peculiar curving of the sides of valve. It shows also the prominence of the dorsal keel.

(The capsule of fig. 17 is somewhat light colored for one which has been long deposited. Old capsules are usually greenish black in color.)

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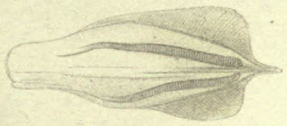

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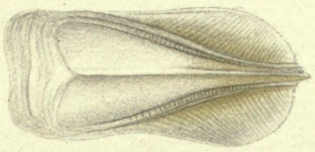

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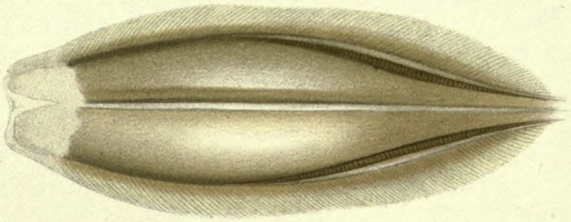

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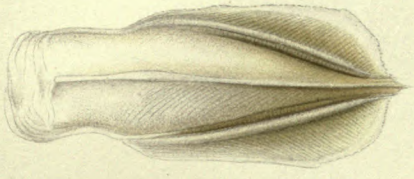

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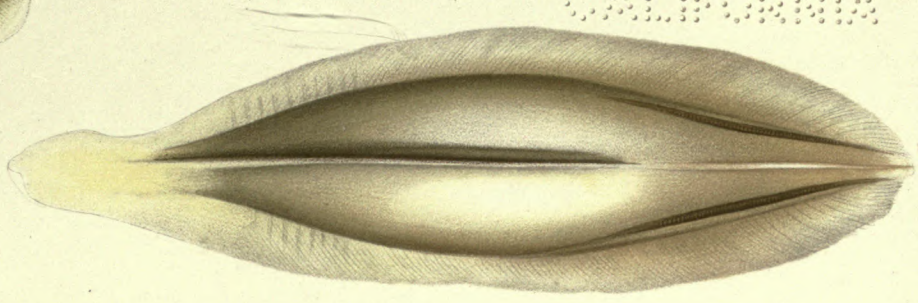

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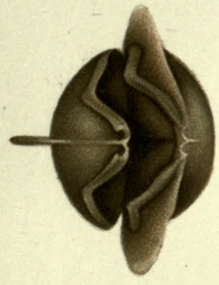

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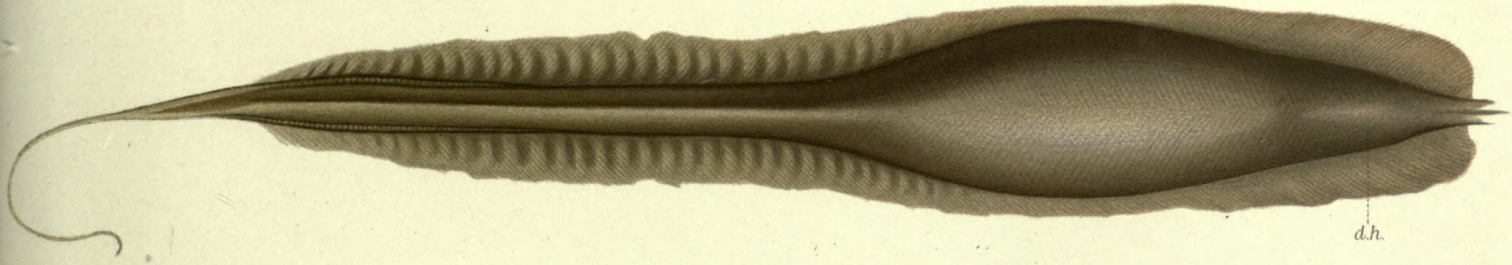

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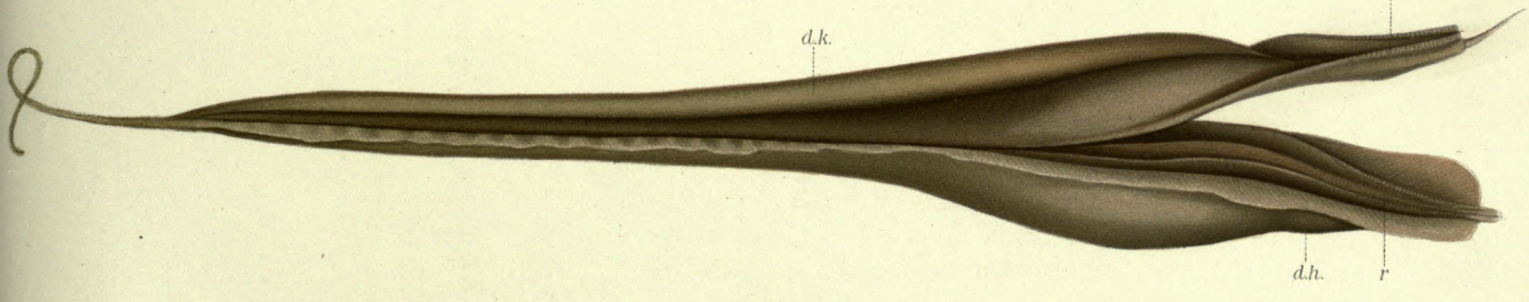

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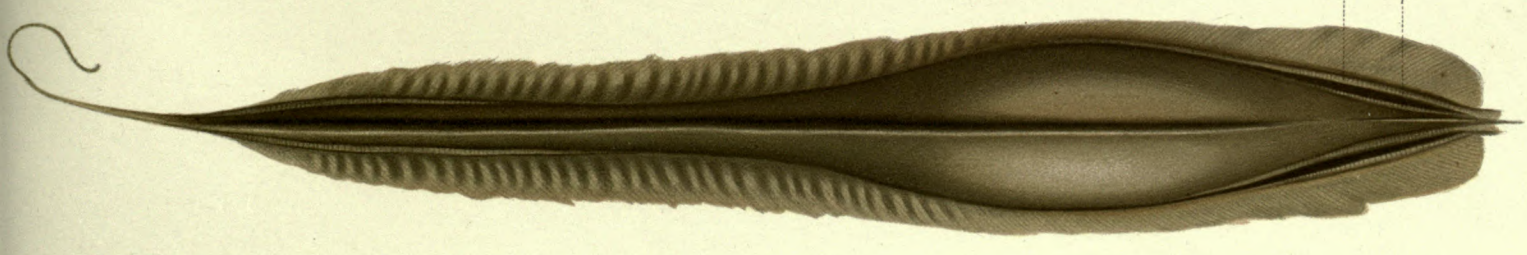

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Plate IV.

Stages of Fertilization, Segmentation, and Blastula.

(Preparations magnified about 15 diameters. All drawings from fresh material. Figs. 22 to 28 from camera drawings of embryos which had been removed from the egg and viewed as transparent objects.)

Fig. 18.—Late stage of fertilization. The oblong shape of the germinal area is due to artifact. The preparation illustrates the number and size of the entrance pits of spermatozoa and the extent of the marginal groove.

Fig. 19.—Later stage of fertilization. This indicates the extent of the marginal groove and the difference in size of the entrance pits of the spermatozoa.

Fig. 20.—Stage showing in surface view a single furrow. As already noted, however, this stage is not one of first segmentation, since it contains several segmentation nuclei. Surrounding the germinal area is a narrow groove margined outwardly by eminences containing sperm nuclei.

Fig. 21.—Stage similar to foregoing, but showing at the surface four "blastomeres."

Fig. 22.—Stage of early segmentation. Here the marginal areas containing sperm nuclei are far less conspicuous.

Fig. 23.—Stage similar to the preceding.

Fig. 24.—Stage of segmentation.

Fig. 25.—Stage of late segmentation. Blastomeres in resting stage.

Fig. 26.—Stage of late segmentation.

Fig. 27.—Stage of late segmentation. The darker color of the central blastomeres indicates a greater depth in this region of the germ.

Fig. 28.—Blastula. In this stage inter-blastomeral lines were traced over the light-colored circumgerminal ring.

Fig. 29.—Blastula. Viewed as an opaque object, and showing a sharply marked boundary between the blastoderm and the circumgerminal ring.

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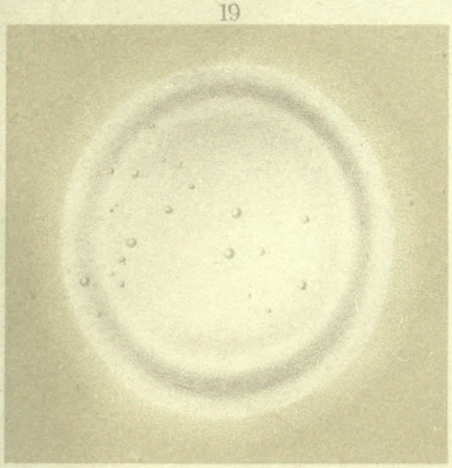

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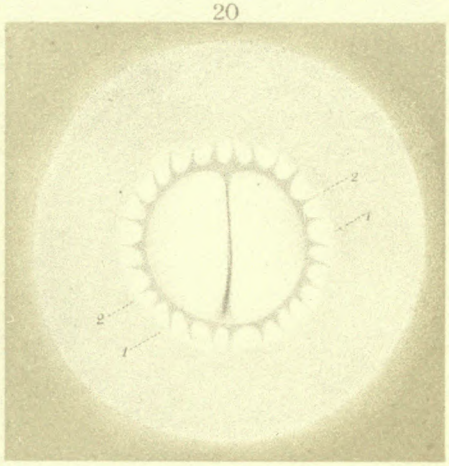

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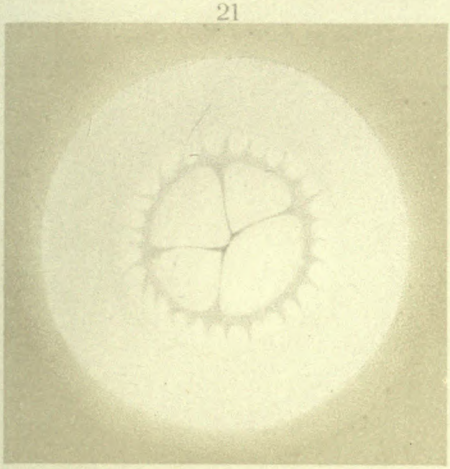

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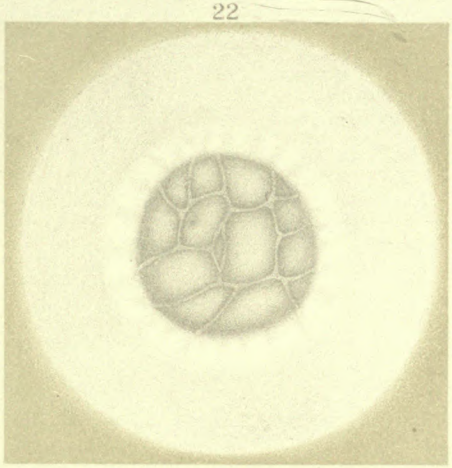

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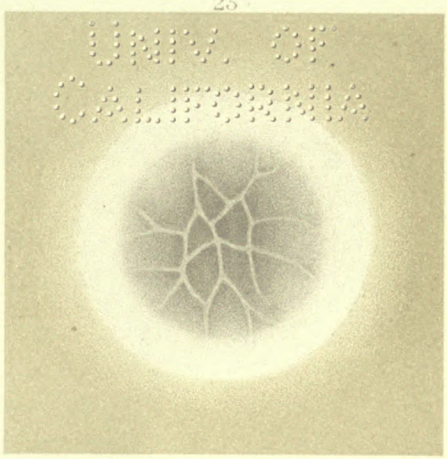

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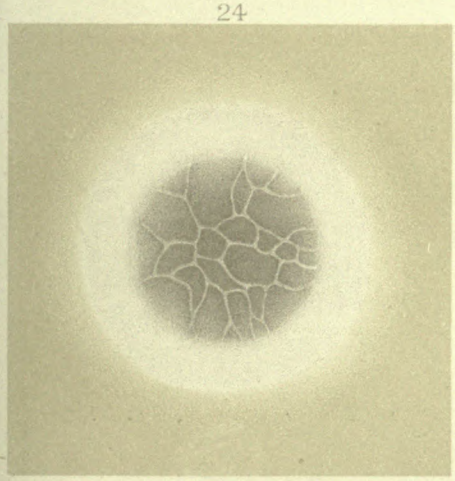

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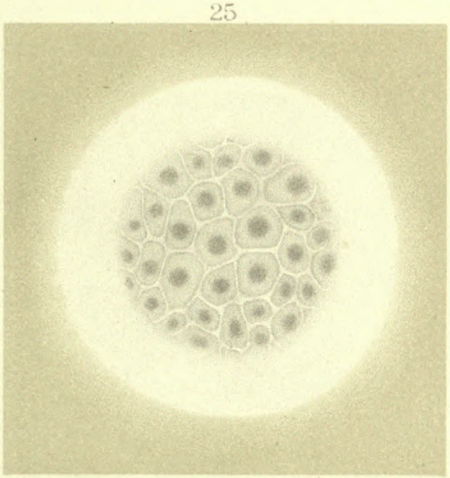

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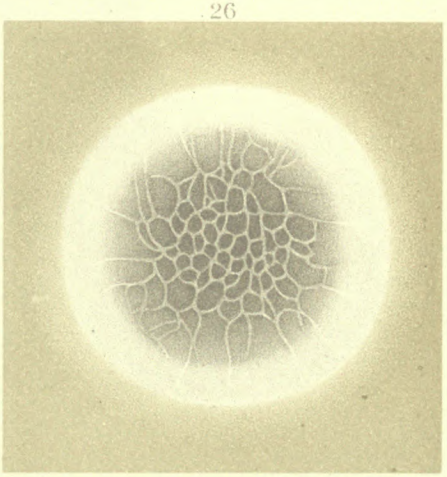

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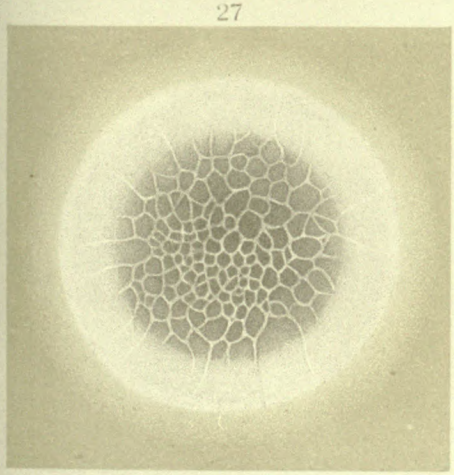

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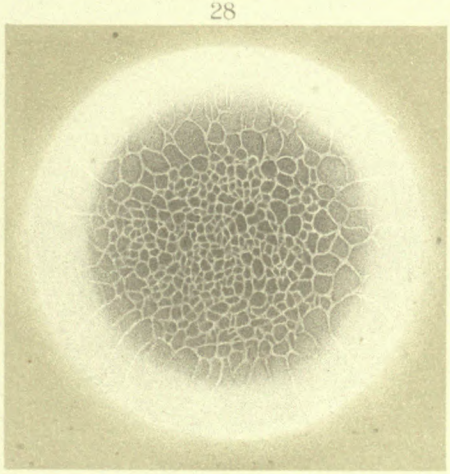

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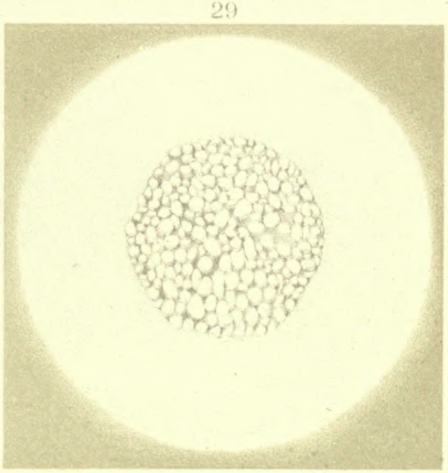

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Plate V.

Blastula, Gastrulæ, and Early Embryos.

(Preparations magnified about 15 diameters. In Figs. 30-34 the circumgerminal zone has been inaccurately lithographed; it should appear less conspicuous, its outer margin merging insensibly into the surrounding yolk.)

Fig. 30.—Late blastula, showing especially the extent of the circumgerminal ring and its irregular margin.

Fig. 31.—Early gastrula. The transverse shadow at the lower end of the germinal area represents the beginnings of the archenteric cavity.

Fig. 32.—Early gastrula, showing the extent of the archenteric space.

Fig. 33.—Gastrula, showing the appearance of the head region of the embryo. In this preparation merocytes could be distinguished in the outer part of the circumgerminal ring.

Fig. 34.—Gastrula, showing the early embryo and the extent of the segmentation cavity.

Fig. 35.—Gastrula, slightly older, showing the early vascularization of the blastoderm.

Fig. 36.—Gastrula, showing early embryo at a stage corresponding with Balfour's stage C in the shark.

Fig. 37.—Blastoderm, showing embryo at a stage corresponding with Balfour's stage F in the shark.

Fig. 38.—Blastoderm and embryo at a stage corresponding with Balfour's stage G in the shark.

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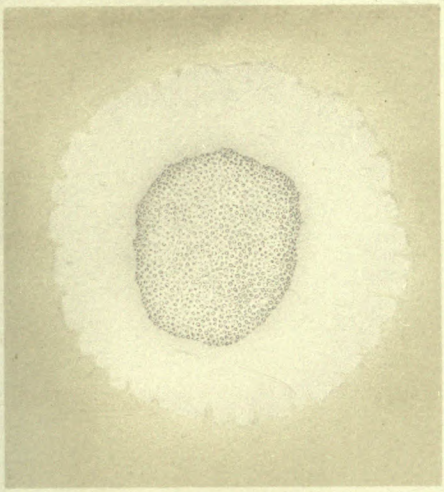

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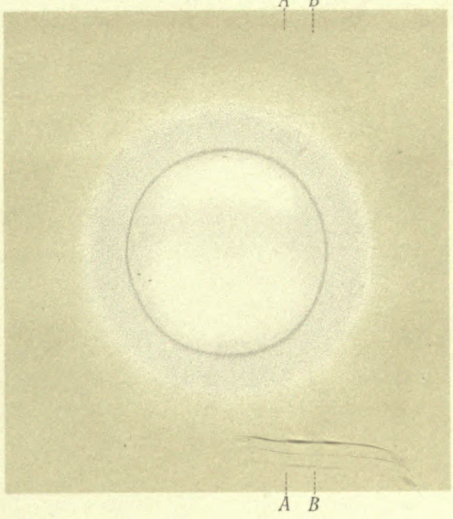

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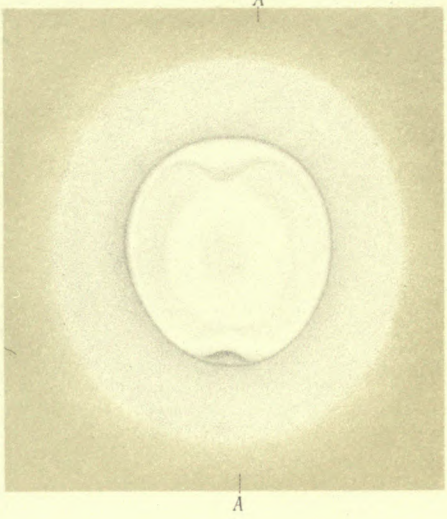

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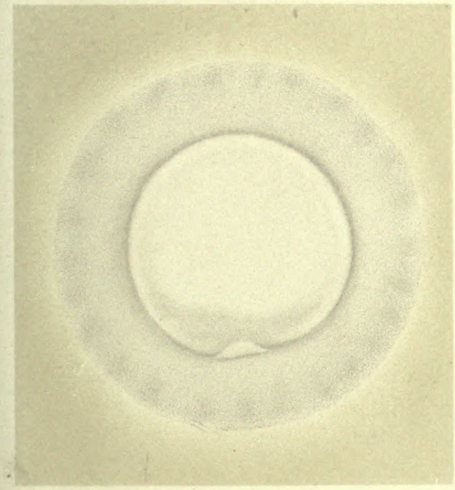

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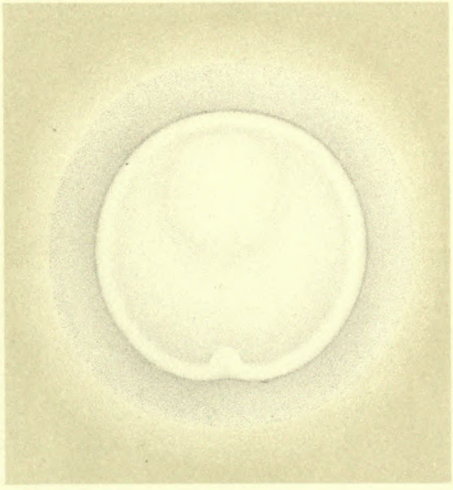

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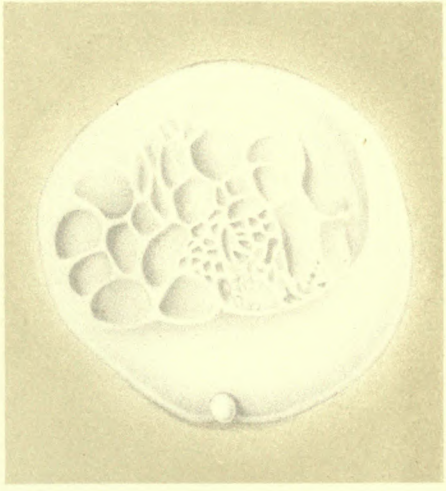

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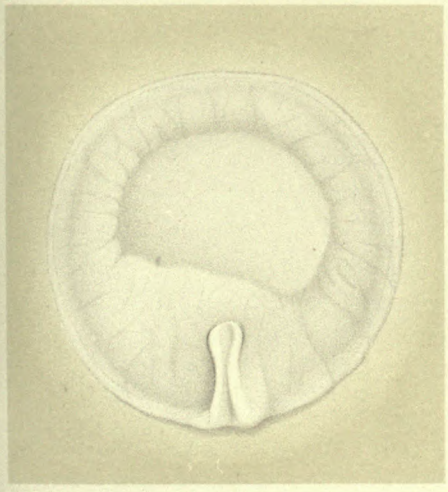

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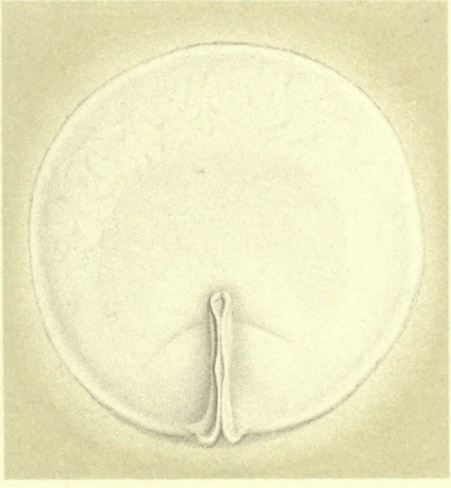

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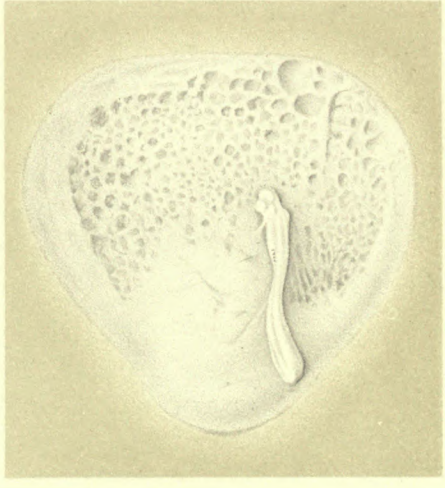

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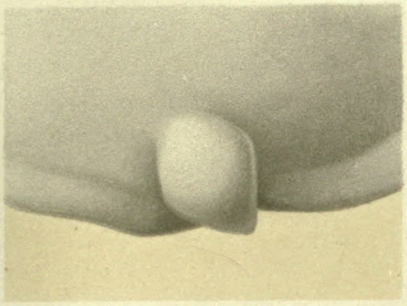
Plate VI.

Details of Early Embryos.

a.	Archenteron.	*n.*	Neurenteric opening.
ec.	Ectoderm.	*op.*	Optic vesicle.
ent.	Entoderm.	*pn.*	Pronephric region.
g^{i}. g^{ii}.	First and second gill-clefts.	*v. i.*	Vitello-intestinal vein.
h.	Heart.		

Fig. 39.—Detail of embryo shown in plate I, fig. 35, viewed as an opaque object.
Fig. 39 *a-e.*—Same embryo viewed in various positions as transparent object.
Fig. 40.—Embryo shown in plate VI, fig. 36, viewed as a transparent object.
Fig. 41.—Embryo shown in plate VI, fig. 37, viewed as a transparent object.
Fig. 41 *a.*—Embryo shown in plate VI, fig. 38, viewed as an opaque object.
Fig. 41 *b.*—Embryo shown in plate VI, fig. 38, viewed as a transparent object.

39



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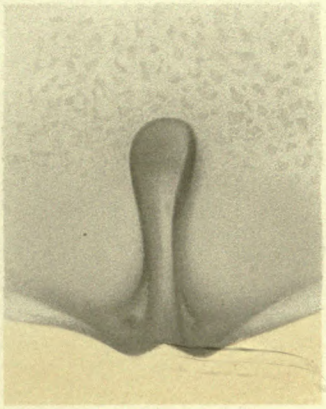

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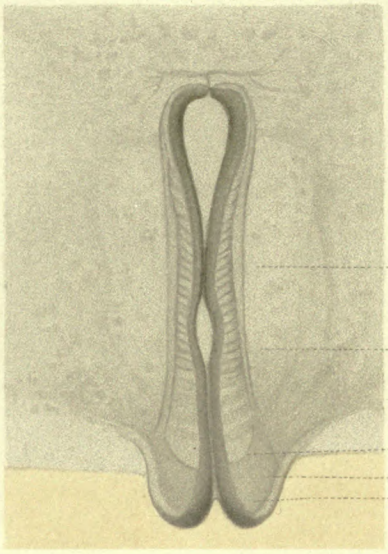

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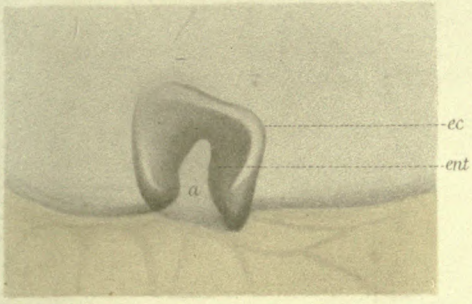

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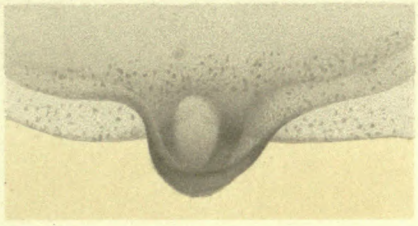

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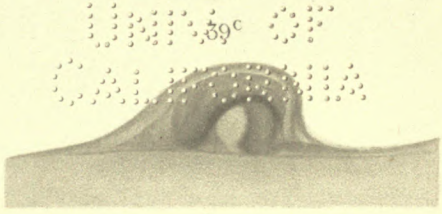

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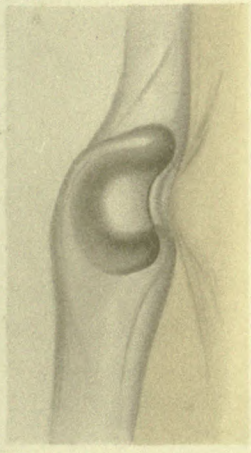

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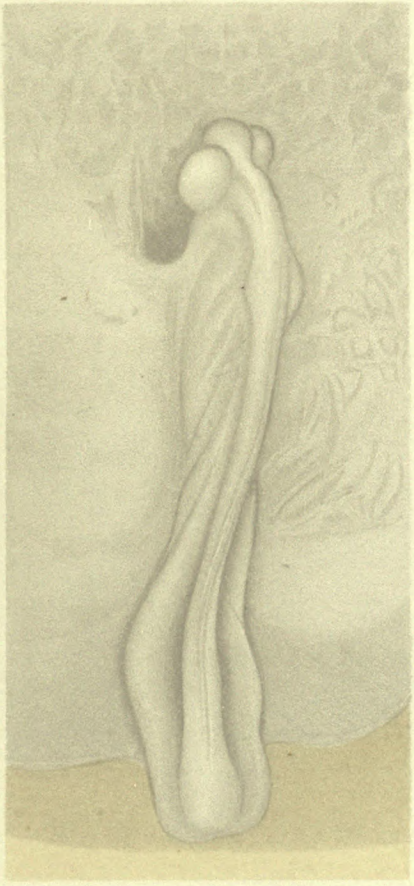

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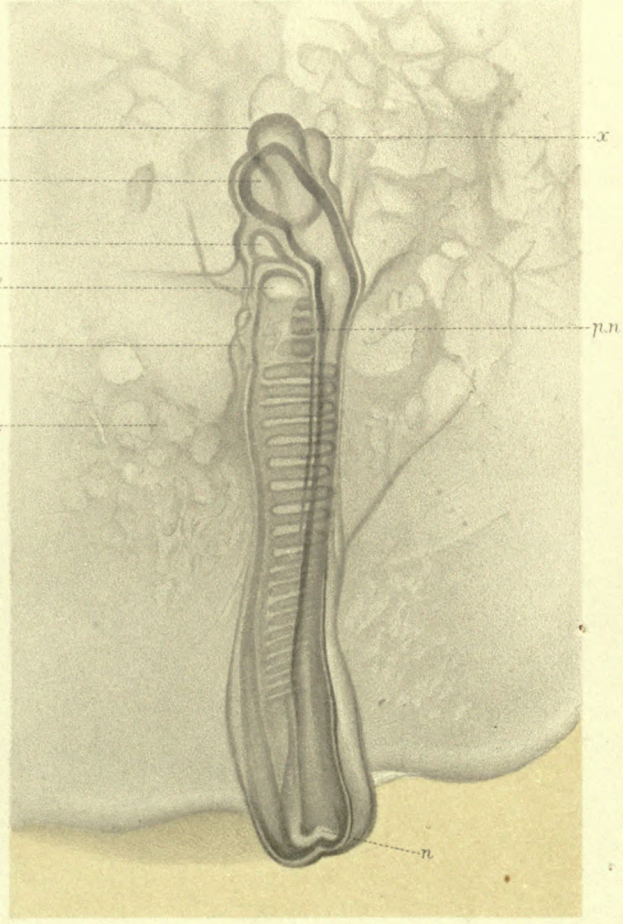


39E

Plate VII.

Later Embryos.

(Preparations magnified about 25 diameters.)

a.	Anus.	*ot.*	Otic vesicle.
at.	Atrium.	*ot. o.*	External opening of otic vesicle.
b.	Epiphysis.	*p.*	Pineal outgrowth.
c.	Conus arteriosus.	*p. a. g.*	Postanal gut.
c. e.	Caudal eminence.	*pn.*	Pronephros.
c. v.	Caudal vein.	*pn. d.*	Pronephric duct.
g', *g''*.	Gill slits.	*p. f.*	Pectoral fin.
k.	Cephalic knob.	*s.*	Spiracle.
op.	Optic vesicle.	*s. v.*	Sinus venosus.
		v.	Ventricle.

Fig. 42.—Embryo, age about 25 days, corresponding to Balfour's stage G (+) of shark. This embryo bent during the process of fixation. It shows especially well the knob-like outgrowth, *k.* in the region of the forebrain.

Fig. 42 *a* and *b*.—Anterior region of preceding embryo. Shown in nearly lateral and in dorsal aspect.

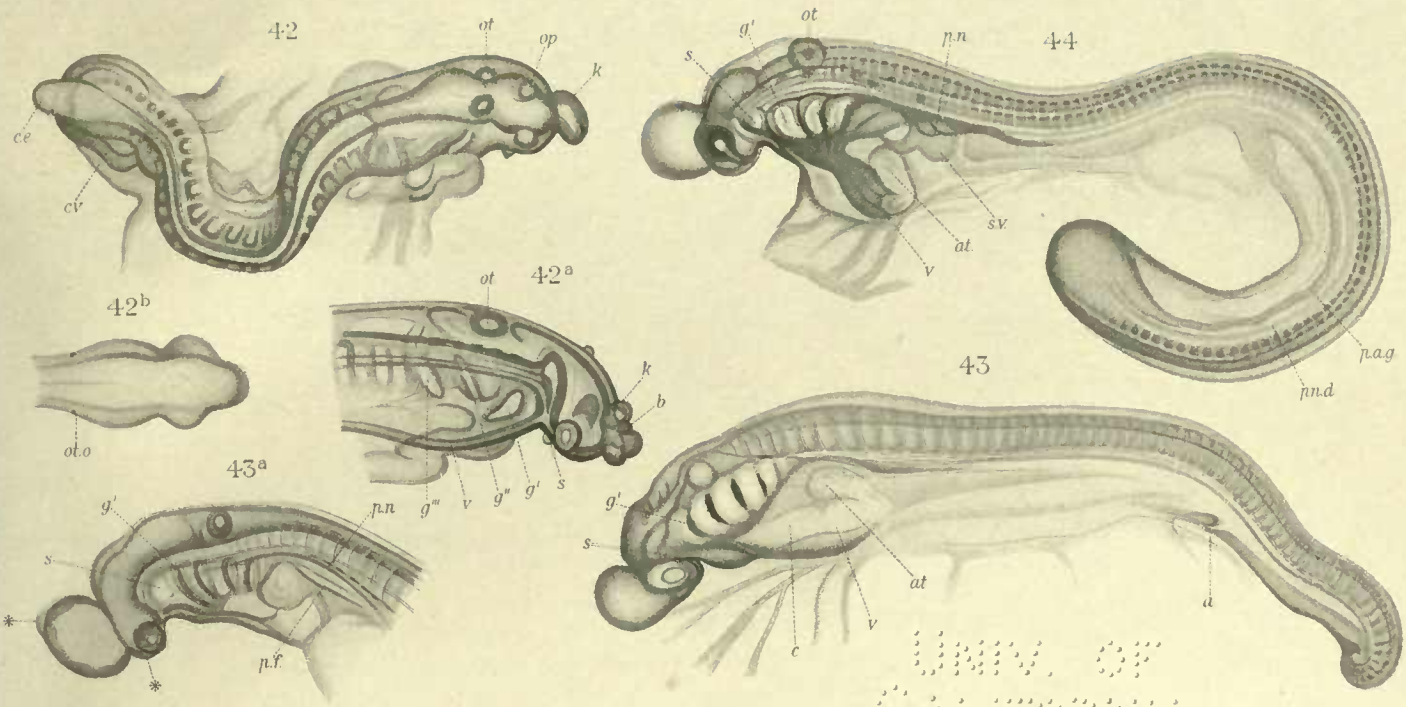
Fig. 43.—Embryo, age about 29 days, corresponding approximately to Balfour's stage I in shark.

Fig. 43 *b*.—Anterior region of specimen similar to preceding.

Fig. 44.—Embryo, age about 31 days, corresponding approximately to Balfour's stage J in shark. It shows a bulbous caudal thickening.

Fig. 45.—Embryo, age about 40 days, corresponding approximately to Balfour's stage K in shark. The circular area under the letters *g.' g.''* was found to be artifact.

Fig. 46.—Embryo, age about 45 days, somewhat more advanced than Balfour's stage L in shark. At the time of fixation the embryo probably twisted, so that its axis came to lie nearly parallel to the neighboring margin of the blastoderm. (Length of embryo 20 mm.)



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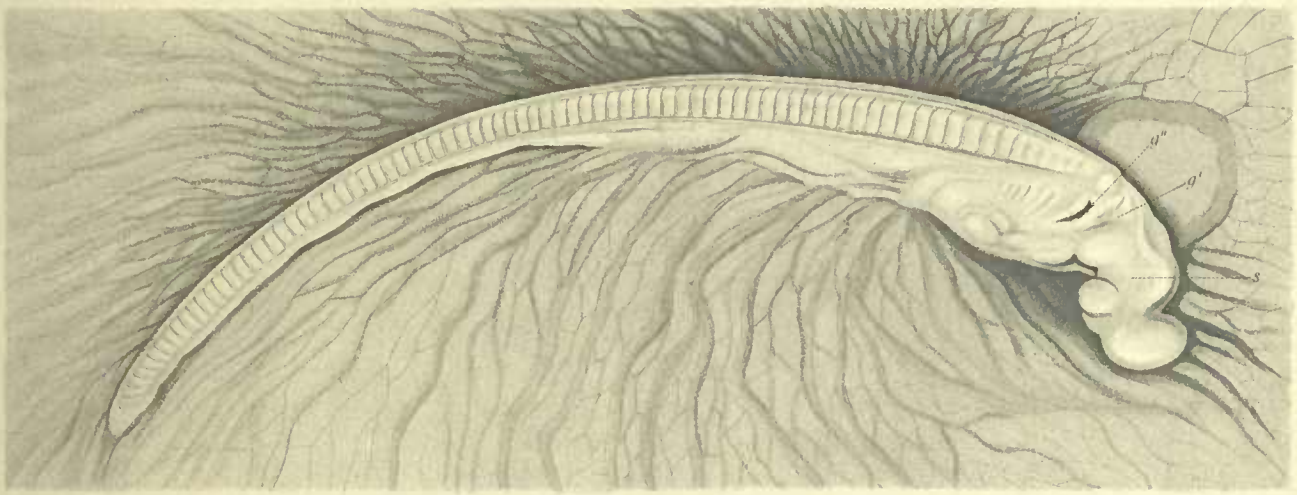

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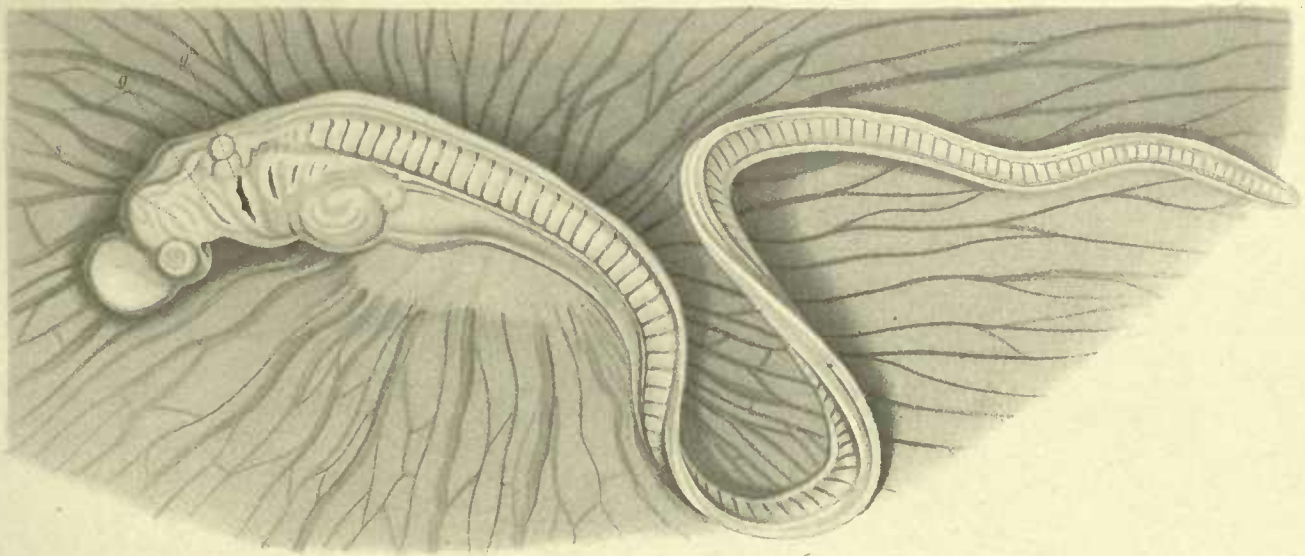

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Plate VIII.

Embryos of Chimæra colliei.

ch.	Notochord.	*sp.*	Spiracle.
n.	Neural tube.	*x.*	Irregularity in line of postanal gut. Possibly artifact.
n. c.	Neurenteric canal.	*y.*	Yolk.
p. a. g.	Postanal gut.	*y. s.*	Stalk of yolk-sac.

Fig. 42 *c.*—Ventral aspect of the head region of specimen shown on plate VII, fig. 42. This indicates especially the extent of the stomadeal invagination.

Fig. 46 *a.*—Detail of tip of tail of specimen shown in plate VII, fig. 46. It illustrates especially the character of the caudal knob and the extent of the postanal gut.

Fig. 47.—Embryo and blastoderm shown attached to irregular mass of yolk. The embryo is of the stage shown in plate VII, fig. 44. It will be seen that a deep crease marks the line of separation of blastoderm and yolk, *y.*

Fig. 47 *a*, *b.*—Figures showing the foregoing specimen in natural size. These give an idea of the extent of the yolk mass around which the blastoderm is growing.

Fig. 47 *c.*—Margin of blastoderm in the region which, in fig. 47, is concealed by the tail. It is here slightly nicked, and a line of fusion can be traced in the direction of axis of embryo.

Fig. 48.—Embryo of stage shown in plate VII, fig. 45. The blastoderm has by this stage almost entirely inclosed the yolk mass noted in fig. 47. A small portion of the yolk is, however, seen in lower part of figure. The figure also shows, although indistinctly, a line of fusion passing from the embryo in the direction of the rim of the blastoderm.

Fig. 48 *a.*—Preceding specimen shown in posterior aspect. This indicates the extent to which the rim of the blastoderm has inclosed the yolk. The irregularity in its margin is due probably to artifact. In the yolk itself masses can be distinguished, even under a low power, which suggest separate blastomeres. The exposed surface of the yolk is somewhat irregular, suggesting that a portion of the yolk material has recently become detached. The blastomeres themselves are loosely associated, so that some of them could be removed with dissecting needles. Their peripheries are not quite as distinct as the present figure indicates.

Fig. 49.—Late embryo. Age unknown (probably five or six months), corresponding approximately to Balfour's stage N in shark. Although this specimen was examined living, and was apparently uninjured, its body cavity was filled with blood cells. Observe also the enlarged blood-knots in the external gills and the position of the spiracle denoted in this figure by the small red spot immediately above the rim of the upper jaw. (Embryo's length 35 mm.)

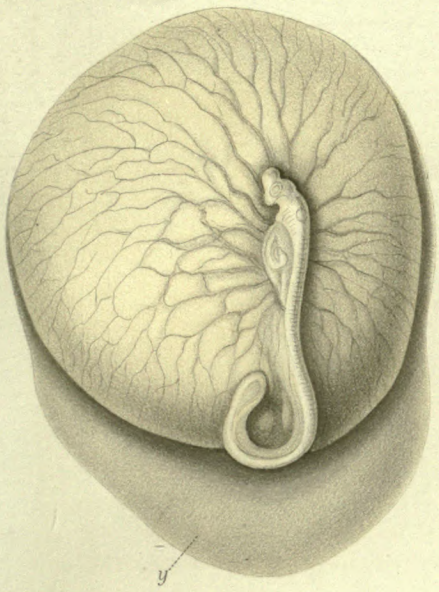
Fig. 49 *a.*—Dorsal aspect of preceding specimen. This pictures more clearly the blood-knots of the external gills.

Fig. 49 *b.*—Ventral aspect of preceding specimen. This shows especially the masses of yolk, *y*, attached to the external gills; also the point of attachment of the stalk of the yolk sac, *y. s.*

Fig. 49 *c.*—Detail of facial region of preceding specimen, indicating the extent to which the gill arches protrude at the side of the head. The gill filaments are cut away, but from their bases one observes that they occur only on the anterior rim of each gill slit.

Fig. 49 *d.*—Lateral aspect of preceding specimen. This pictures again the gill region from which the external filaments have been removed. The spiracle, *sp.*, is seen immediately under the eye.

47



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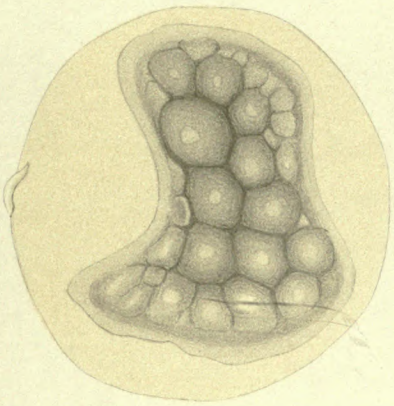

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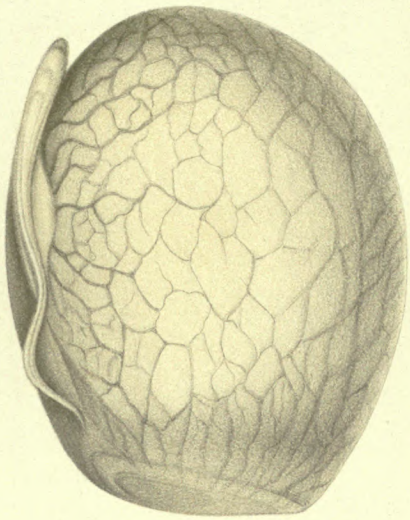

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47a

47b

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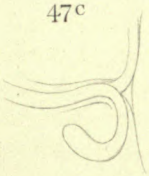

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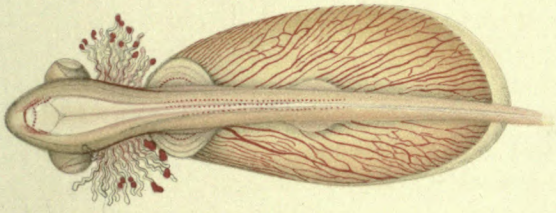

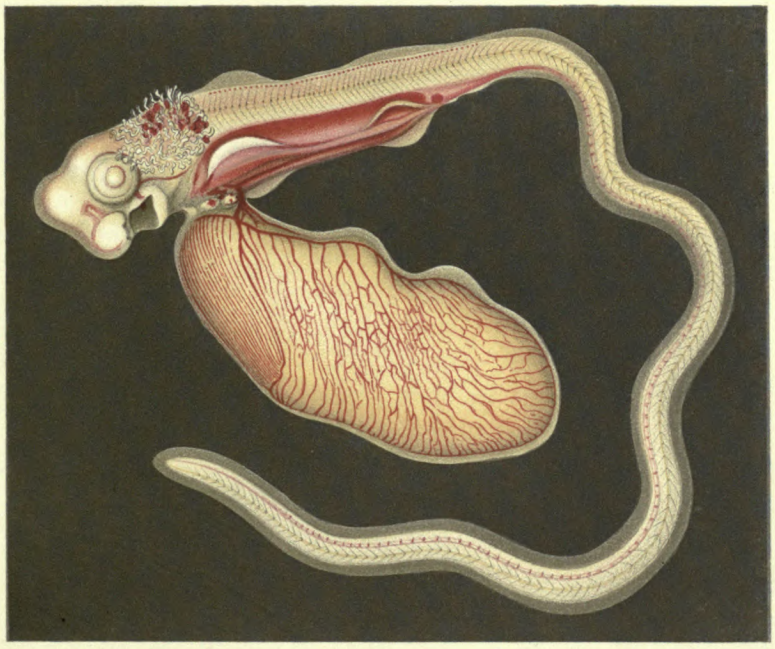

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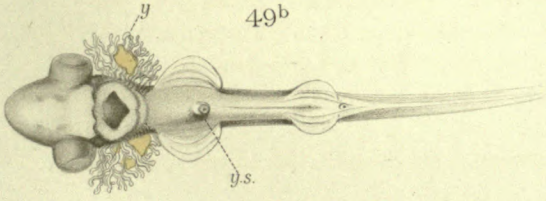
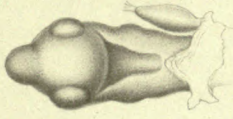


49c

42c



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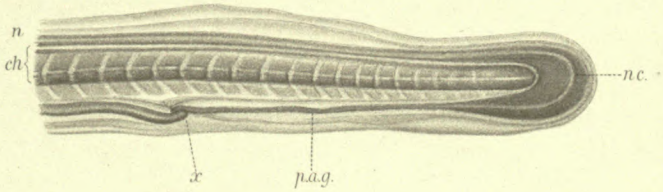

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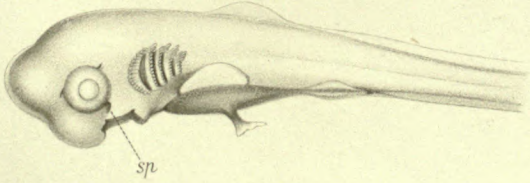


Plate IX.

Late Embryo of Chimæra colliei.

a. cl.	Antero-pelvic clasper.	*mix.*	Mixipterygium.
a. d. p.	Anterior dental plate.	*p. d. p.*	Palatine dental plate.
f. o.	Frontal organ.		

Fig. 50.—Late embryo, age about six months, corresponding approximately to Balfour's stage P in shark. Lateral view. The attachment of small masses of yolk to the side of the embryo is probably artifact. The opercular fold has here been partly cut away, so as to expose the gills. × about 3.

Fig. 50 *a*.—Ventral aspect. External gills removed from the left side.

Fig. 50 *b*.—Dorsal aspect.

Fig. 50 *c*.—Anterior aspect. External gills removed from the left side. Observe particularly the large size of the frontal clasping organ.

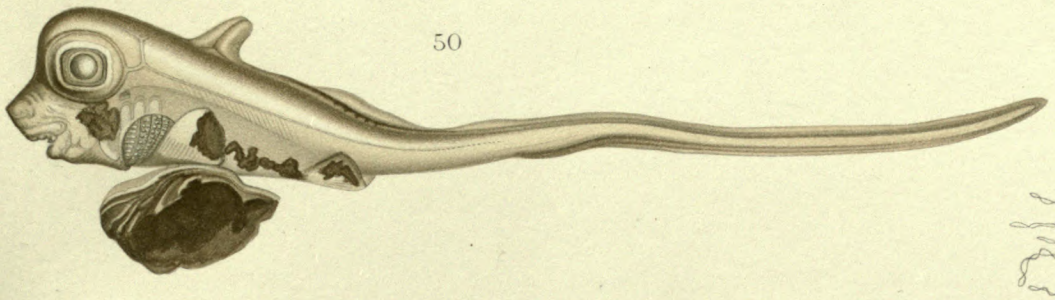
Fig. 50 *d*.—Ventral region, showing extent to which the opercular fold has overgrown the gill lamellæ. A detail is given as to the origin of the external filaments.

Fig. 50 *e*.—Region of the mouth. This shows especially the appearance of the sensory canals and the early condition of the dental eminences and of the labial cartilages.

Fig. 50 *f*.—Ventral fin, showing the early condition of the mixipterygium and of the antero-ventral clasping organ.

Fig. 50 *g*.—External gill filaments, giving detail of vein and artery.

50



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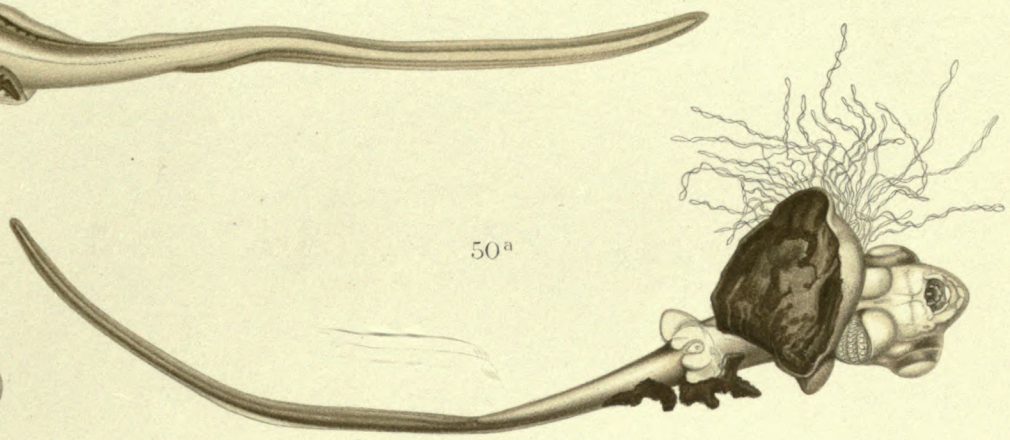

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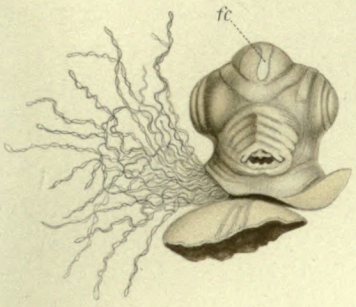

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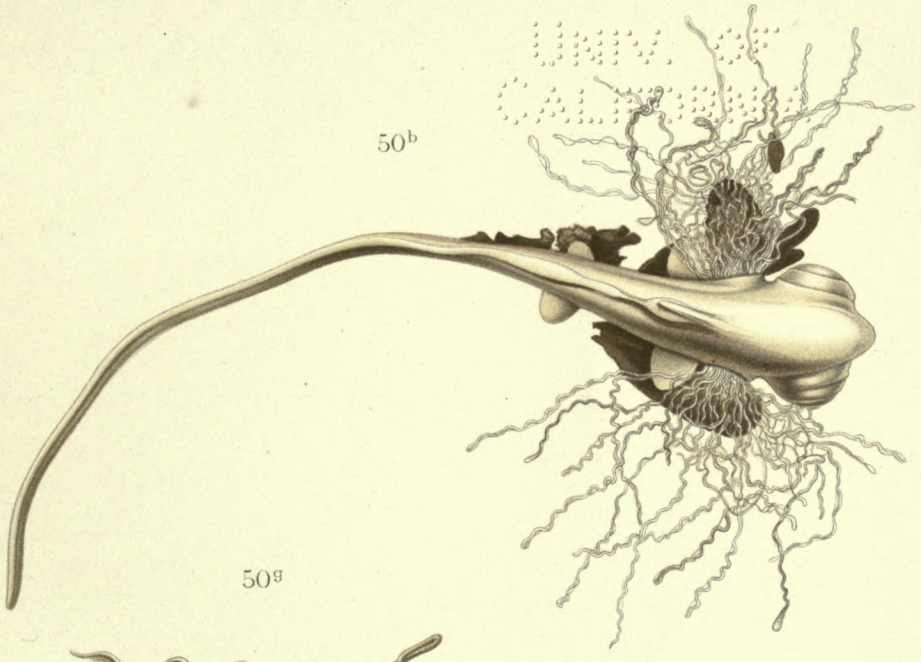

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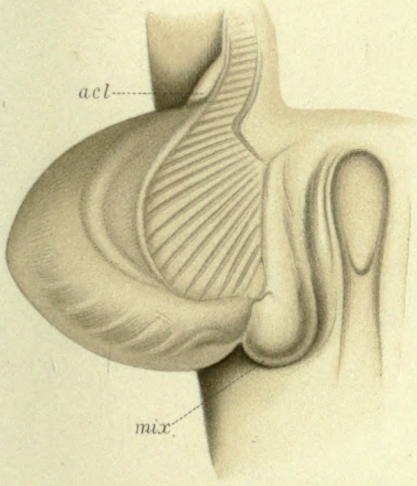
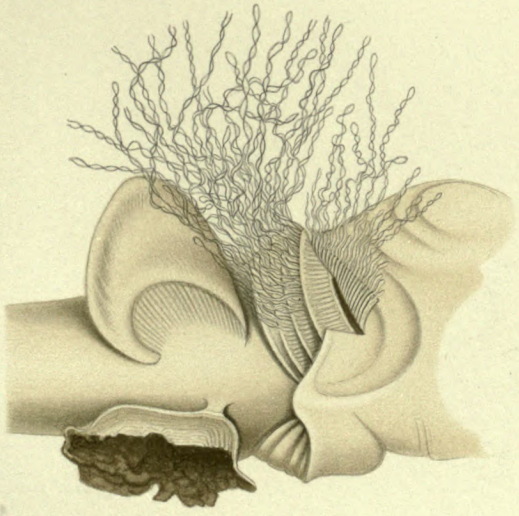


50g

50d



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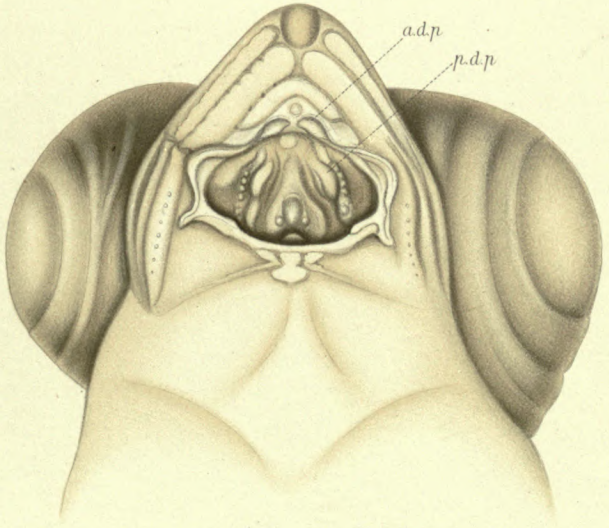

Plate X.

"Larvæ" of Chimæra colliei.

These specimens were dredged off the Californian coast by the U. S. Fish Commission steamer *Albatross*, in water of about 300 fathoms. Figures are of nearly natural size.

Fig. 51.—Newly hatched young. Length about 10 cm. This shows especially the great width of the pectoral fin, the relatively large eye, and the lack of lateral coloration.

Fig. 51 *a*.—Dorsal aspect of foregoing specimen. Observe particularly the large size of the openings of the auditory organ, *au*.

Fig. 51 *b*.—The ventral aspect of foregoing specimen. At *y. s*. is shown the scar, marking the point of entrance of the yolk-sac.

Fig. 52.—Young of about 12.5 cm. This specimen shows a marked differentiation of the dorsal fin, also noteworthy changes in coloration.

Fig. 52 *a*.—Dorsal aspect of foregoing specimen.

Fig. 53.—Young, 18.5 cm. in length. This exhibits an extreme degree of pigmentation.

Fig. 53 *a*.—Dorsal aspect of foregoing specimen.

Fig. 53 *b*.—Ventral aspect of foregoing specimen.

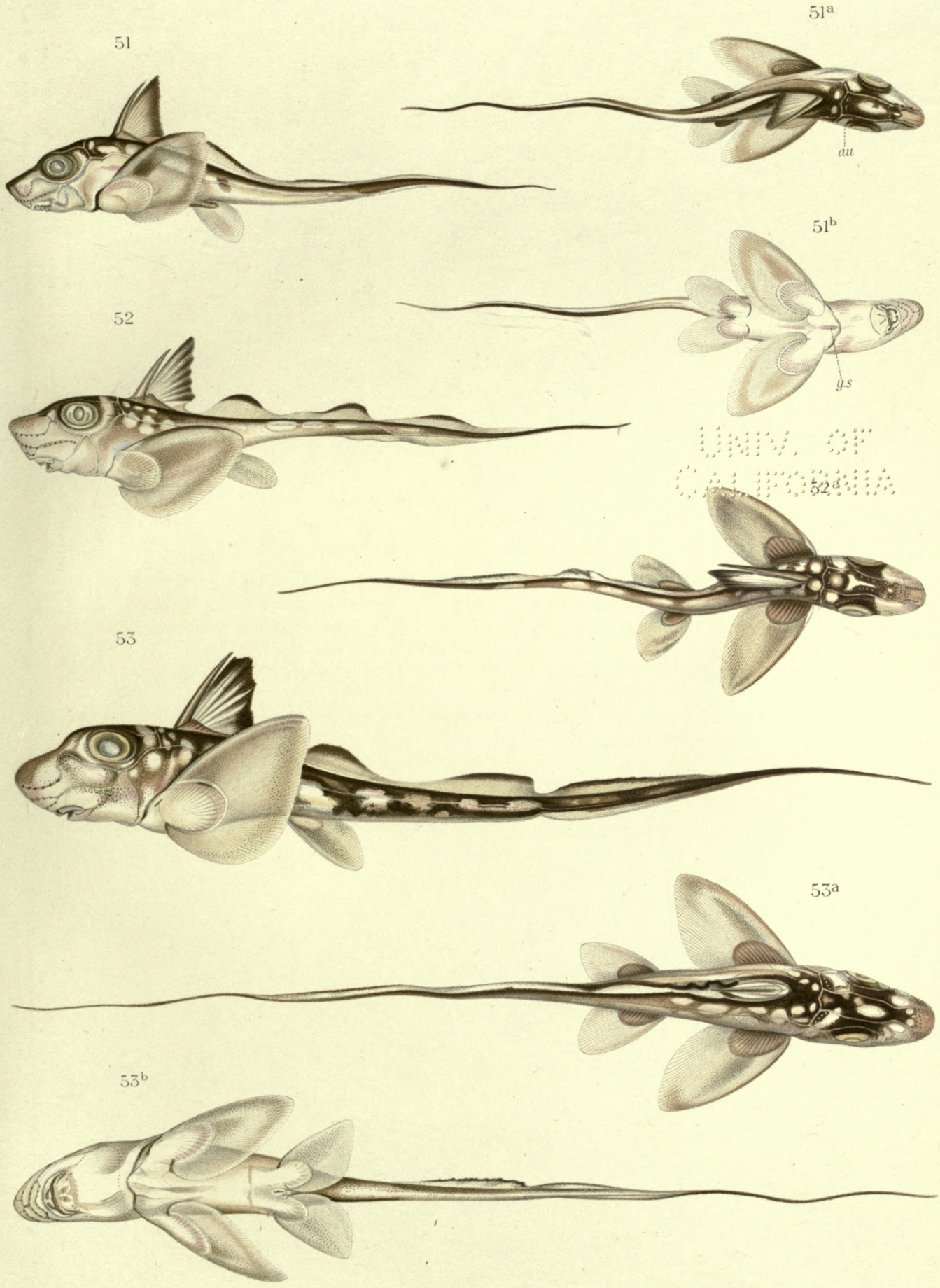

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Plate XI

Immature Specimen of Chimæra colliei.

This was drawn from a freshly taken specimen and is intended to represent the fish in its natural colors ; it does not, however, give an adequate idea of the brilliantly metallic shades of the living fish, or of the translucency of the snout region. At this stage the fins are deeply pigmented. Natural size.

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